

PDF hosted at the Radboud Repository of the Radboud University Nijmegen

The following full text is a publisher's version.

For additional information about this publication click this link.

<http://hdl.handle.net/2066/141062>

Please be advised that this information was generated on 2017-12-05 and may be subject to change.

Social learning dynamics in chimpanzees
Reflections on animal culture

Edwin van Leeuwen

Copyright © 2015 by Edwin J. C. van Leeuwen

The research reported in this thesis was supported by the Comparative Cognitive Anthropology research group of the Max Planck Institute for Psycholinguistics and the Max Planck Institute for Evolutionary Anthropology.

Cover image: Kathy grooms Val while Val has a straw of grass sticking out of his left ear (at the Chimfunshi Wildlife Orphanage Trust).

ISBN: 978-90-76203-66-9

Social learning dynamics in chimpanzees

Reflections on animal culture

Proefschrift

ter verkrijging van de graad van doctor
aan de Radboud Universiteit Nijmegen
op gezag van de rector magnificus prof. dr. Th.L.M. Engelen,
volgens besluit van het college van decanen
in het openbaar te verdedigen op dinsdag 16 juni 2015
om 14:30 uur precies

door

Eduard Johannes Cornelis van Leeuwen
geboren op 19 december 1980
te Hilvarenbeek, Nederland

Promotoren:

Prof. dr. Stephen C. Levinson

Prof. dr. Daniel B. M. Haun (Universität Leipzig, Duitsland)

Copromotor:

Dr. Katherine A. Cronin (Lincoln Park Zoo, Verenigde Staten)

Manuscriptcommissie:

Prof. dr. Harold Bekkering (voorzitter)

Prof. dr. Carel van Schaik (Universität Zürich, Zwitserland)

Dr. Rachel Kendal (Durham University, Verenigd Koninkrijk)

Table of contents

Chapter 1	Introduction	3
Chapter 2	Neighbouring chimpanzee communities show different preferences in social grooming behaviour	29
Chapter 3	A group-specific arbitrary tradition in chimpanzees (<i>Pan troglodytes</i>)	47
Chapter 4	Conformity in nonhuman primates: Fad or Fact?	59
Chapter 5	Chimpanzees flexibly adjust their behaviour in order to maximize payoffs, not to conform to majorities	79
Chapter 6	Conformity without majority? The case for demarcating social from majority influences	103
Chapter 7	Human children rely more on social information than chimpanzees	125
Chapter 8	Conclusions and General Discussion	137
	References	155
	Samenvatting	177
	Acknowledgements	183
	Curriculum Vitae	187
	List of Publications	189
	MPI Series in Psycholinguistics	191

“Without culture, and the relative freedom it implies, society, even when perfect, is but a jungle. This is why any authentic creation is a gift to the future.”

(Albert Camus, 1942)

Introduction

Chapter 1

Social learning endows animals with the opportunity to obtain knowledge about environmental contingencies without being physically involved (thus minimizing energy expenditure and risk) and forms the core of cultural diversification (Richerson & Boyd, 2005). Where the former social learning aspect pertains more directly to animals' survival, the latter aspect has been emphasized in discussions on the uniqueness of human culture (e.g., see Galef, 1992; de Waal, 2001; Whiten & van Schaik, 2007). The term 'cultural panthropology', as a specific variant of 'cultural primatology' (see de Waal, 1999; McGrew, 2004), refers to the evolutionary anthropological study of cultural phenomena by focusing on the *Pan* species, namely chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) (Whiten et al., 2003), and will be guiding the current scientific endeavour. Specifically, in this dissertation, I will investigate the social learning dynamics of chimpanzees with the aim to gain a further understanding of chimpanzee behaviour and to shed light on the meaning of 'culture'.

Learning dynamics, and why they are interesting

Learning in general is a special type of behavioural plasticity that allows individuals to transcend their genetic predispositions and attune their phenotypes to their environment (Brown, 2013; Dukas, 2013). By being able to contingently nudge interactions with the physical and social environment and integrate these adjustments into behavioural templates, organisms have a means to follow shifting optima peaks inherent to changing environments and thus to actively increase their chances of survival and reproduction. As many physical and social environments are characterized by (gradual) change, many organisms found on earth have evolved the capacity to learn (Heyes, 2012; Dukas, 2013).

Interestingly, some species have the capacity to extract information from their environments by means of two distinct learning modes: individual and social learning. Where individual learning refers to the process of obtaining information through trial-and-error sequences, social learning refers to learning from other agents interacting with the environment. These interactions can provide information about the affordances of the inanimate world or the interacting agents themselves, even beyond the scope of present time (Heyes, 1994; Heyes, 2012). As alluded to in the first sentence of this introduction, the key feature of social learning is the acquisition of information through *observation* of conspecifics, which implies that environmental affordances and contingencies need not be experienced by the agent itself for an understanding of their existence (Bandura, 1971). Compared to individual learning, this feature of social learning alleviates two fitness-affecting strains – time and risk – and it is for this reason that social learning has received considerable theoretical attention within the realm of understanding learning preferences in (social) animals (e.g., see Laland, 2004; Richerson & Boyd, 2005; Kendal et al., 2009). If social learning bestows superiority over individual learning, through its shortcut on trial-and-error sequences, then, given the strong selection pressures caused by the vicissitudes of the environment (*sensu* (Wallace, 1858; Darwin, 1859), why would any social animal still engage in individual learning (e.g., Rogers, 1988)? The answer lies in the fact that individual learning yields more reliable and up-to-date information about the environment than social learning ever could (Richerson & Boyd, 2005). Particularly when environments change such that their optimal usage requires an on-going process of adjusting strategies, it is not hard to imagine how first-hand samplers obtain more adequate information than second-hand learners. Thus, in the realm of a crucial adaptive challenge, an intriguing trade-off exists between accurate, yet costly individual learning and relatively inaccurate, yet cheap social learning.

Scholars mesmerized by this trade-off have used mathematical models to try and predict which mixture of learning tactics would be most adaptive and viable in terms of evolutionary principles (e.g., Cavalli-Sforza & Feldman, 1981; Boyd & Richerson, 1985). They found that contrary to the widespread belief that

social learning exists because it yields adaptive benefits, social learning did not increase individuals' average fitness in the initial models. In other words, populations in which individuals could learn both individually and socially would not thrive better than populations characterized solely by individual learners, despite the fact that social learning inherently bypasses the costs of individual learning and was thus expected to increase the average fitness in the population. This oddity became known as Roger's paradox (Rogers, 1988; also see Richerson & Boyd, 2005). Not until the models were refined by modifying parameters like differential learning costs, uncertainty as to which behaviour will be the most rewarding, and the capacity to evaluate the adaptive value of the available behavioural variants was Roger's paradox resolved, meaning that social learning was confirmed as a fitness enhancing capacity (Boyd & Richerson, 1995; Kameda & Nakanishi, 2003; Enquist et al., 2007; Eriksson et al., 2007; Rendell et al., 2010). Importantly, this mathematical work culminated in the identification of the circumstances under which animals would be expected to learn socially, i.e., when it would be adaptive for them to do so. Similarly, biases for learning from certain (groups of) individuals were distilled from the models and in conjunction these 'when' (circumstances) and 'whom' (individuals) predictions condensed into 'social learning strategies' (Laland, 2004). One of these predicted strategies pertains directly to the emergence of group differences, which forms an essential part of any definition of 'culture' (see next section). This strategy entails the adoption of the most common behaviour in the group, or more specifically, the behaviour displayed by the majority of group members. Through its intimate link with culture, this social learning strategy also referred to as 'conformity' will be key to my investigations into the social learning dynamics of chimpanzees. Similarly, as 'cultural' group differences by definition consist of socially-transmitted behaviours, I will additionally focus on chimpanzees' relative preferences for social over individual learning, both in comparison to humans and in light of the prediction that social animals should copy the behaviour of others when they are uncertain about the environmental contingencies (i.e., 'copy when uncertain'; see Laland, 2004; Kendal et al., 2009).

In sum, social learning refers to learning by observation and circumvents energetic and risk-related costs in comparison to individual learning. Where individuals have the capacity to learn individually and socially, an adaptive trade-off exists between costly yet accurate individual learning on the one hand, and cheap yet potentially less accurate social learning on the other hand. Within this trade-off, social learning is only expected to evolve as a stable strategy when it is employed selectively. Having preliminarily identified some social learning biases that bear special relevance to the study of culture, I will now continue with a detailed appraisal of the notion of 'culture' itself.

Culture: its definitions and characteristics

Culture has been defined as '.. information capable of affecting individuals' behaviour that they acquire from other members of their species through teaching, imitation, and other forms of social transmission' (Richerson & Boyd, 2005, p. 5). But it has also been defined as '.. that complex whole which includes knowledge, belief, art, law, morals, custom, and any other capabilities and habits acquired by man as a member of society' (Tylor, 1871; in Hill, 2010, p. 324) and 'the way we do things' (McGrew, 2004). And there are many more definitions (e.g., see Whiten & van Schaik, 2007; Mesoudi, 2011; Galef, 2012). This immediately indicates that 'culture' is a difficult phenomenon to study across species. For instance, how can culture in animals be identified when it is defined in anthropocentric characteristics like beliefs and art? However, the shared denominator of these definitions seems to be the social transmission of information; to my knowledge, there are no accounts of culture that do not include social learning (e.g., see McGrew, 2004; Hill, 2010; Boesch, 2013). Thus, to the very least, this pivotal aspect of culture enables the comparative study of culture across species.

There has been sustained interest in this pivotal aspect of culture, because of the idea that social learning permits an auxiliary path through which animals can adapt to their environments. Biological accounts of survival, reproduction and fitness have traditionally focused on evolutionary selection principles (Darwin, 1859), implicitly and later explicitly on the level of genes

(Fisher, 1930; also see Fisher, 2003). Intriguingly, scholars have suggested that these evolutionary principles might similarly apply to the realm of social learning such that parallel to genetic evolution animals may have a 'second inheritance system' through which they can facilitate adaptation (e.g., see Richerson & Boyd, 2005; Whiten, 2005; Sterelny, 2006; Danchin et al., 2011). Social learning might for example bestow the possibility to create niches where none existed (see Laland et al., 2000; Henrich & McElreath, 2003), and facilitate survival when environments, be they ecological or social, become increasingly demanding (Richerson & Boyd, 2005; Whiten & Erdal, 2012). This latter adaptive potential has specifically been assessed in conjunction with the capacity to continually incorporate learned properties into existing behavioural templates so that knowledge cumulates, or 'ratchets up', to the extent that these learned constructs possess a complexity impossible to obtain individually in one life-time (Tomasello, 1999; Richerson & Boyd, 2005; Tennie et al., 2009).

Inspired by this dazzling potential of culture, scholars became interested in the question of whether humans' cultural capacity emerged before or after the split from our last shared ancestor with the *Pan* species (e.g., McGrew, 2004; Whiten, 2011). More specifically, for reasons of obtaining an evolutionary understanding of the emergence of 'culture', ethologists and comparative psychologists have taken up the challenge to study culture in nonhuman animals (henceforth 'animals'). One of the approaches developed to study animal culture has become known as the 'ethnographic' or 'geographic' method (Wrangham et al., 1994; van Schaik et al., 2003). In principle, this method aims at charting behavioural differences across wild populations of animals while simultaneously scrutinizing whether any of the observed variation could be due to genetic or ecological determinants. If the answer to this scrutiny is negative, then the claim that at least part of the observed variation is owing to local conventions, i.e., caused by social learning processes, would be substantiated (also see Whiten et al., 1999). Many putatively cultural behaviours were identified using this method, for instance in capuchin monkeys (Perry et al., 2003), chimpanzees (Whiten et al., 1999) and orang-utans (van Schaik et al., 2003), but also in non-primate species like dolphins (Krützen et al., 2005) and whales (Rendell &

Whitehead, 2001). Critics pointed out, however, that the employed method was not valid for identifying 'culture', as genetic and ecological influences are notoriously hard to rule out from any behaviour observed under wild conditions (Laland & Janik, 2006). Following from these opposed positions on identifying animal culture was a lively discussion informally labelled 'the animal cultures debate' (see Krützen et al., 2007; Laland & Janik, 2007; Boesch, 2013), which will be touched upon in this dissertation.

The extent to which group differences not accounted for by genetic or ecological factors would justify an interpretation in terms of 'culture' is still unclear. We have seen that considerable definitional differences exist across research disciplines with respect to pinpointing culture, and this predicament extends to the realm of ethology, in which culture needs to be operationalized such that at least the possibility exists of identifying it in non-human species (see McGrew, 2004). However, we have also noted that the 'social transmission of information' may play a pivotal role in any definition of culture, which would provide us with a first prerequisite for identifying culture across species (also see McGrew, 2004; Boesch, 2013). This pivotal element of 'culture' has been intimately linked to the ethnographic method earlier mentioned and the social learning biases. Where social learning was found to be adaptive only when used selectively (as in the social learning strategies, see Laland, 2004), the particular bias of copying the behaviour that the majority of group members are using, broadly called 'conformity', has been predicted to be one of the main drivers behind the type of behavioural variation identified by the ethnographic method. In other words, by synchronizing with the majority, individuals tend to move their groups toward behavioural homogeneity, while at the same time increasing the chances of accentuating between-group diversity (e.g., see Boyd & Richerson, 1985). In principle, this means that culture would be an emergent property of the 'social transmission of information' being majority biased. For this reason, conformity to majorities will be a key phenomenon under investigation in this dissertation.

Another relatively agreed-upon element of culture is the spread of the socially obtained information across generations (see Perry et al., 2003; Whiten,

2003; Danchin et al., 2010; Galef, 2012). As alluded to before, by passing on learned information to next generations, cumulative knowledge can emerge which could enable individuals to manipulate their environments in ways far beyond their individual potential (see Richerson & Boyd, 2005). Notably, this cumulative, inter-generational aspect would also demarcate culture from ‘mere’ social learning. Additional characteristics to constitute the ethological concept of culture have been proposed by Perry and colleagues (2003) in terms of the *durability* and *expansion* criteria (Perry et al., 2003; Whiten, 2003), where the former ties ‘culture’ to group-specific behaviour with a minimal longevity, and the latter requires that the behavioural variant should show a pattern of gradual transmission to naïve group members. Acknowledging that this latter criterion resembles the earlier mentioned inter-generational information transmission, these observable elements may in conjunction make up the ethological concept of ‘culture’, which can be summarized by ‘population-specific behavioural patterns that continually expand to group members within and across generations by means of social learning’ (also see Boesch, 2013). This definition will be further elucidated in the first empirical study of this dissertation, which is described in chapter 2.

Social learning and culture in chimpanzees

In response to a plethora of environmental challenges, ranging from foraging to predator avoidance to securing mating success, animals across many taxa have been found to rely on (some form of) social learning (e.g., see Galef & Giraldeau, 2001; Hoppitt & Laland, 2008; Reader & Biro, 2010). The observation that even miniature-brained insects (e.g., Leadbeater & Chittka, 2007) and no-brained bacteria (e.g., Ulvestad, 2007) learn from their conspecifics suggests that social learning is a widespread phenomenon. Aiming at gaining an evolutionary understanding of culture, many scholars have studied the social learning capacities and motivations of the extant primates (see McGrew, 1998; Caldwell, 2009; Price & Whiten, 2012), in particular the chimpanzees (e.g., Whiten et al., 1999; McGrew, 2004; Boesch, 2013) and orang-utans (van Schaik et al., 2003; Krützen et al., 2011). Because humans share the longest phylogenetic history

with the other great apes (bonobos, chimpanzees, gorillas and orang-utans), a comparison of their behavioural tendencies may inform the question of whether the behaviour under scrutiny emerged in the environment of our last shared ancestor or whether it may be a derived trait unique to specific lineages (e.g., see MacLean et al., 2012; cf. Reader & Hrotic, 2012). Focusing on the chimpanzee, there is an interesting story to tell.

Firstly, chimpanzees are a patrilocal species of great ape that live in multi-male multi-female fission-fusion societies, which means that their societies are characterized by patterns of temporary, mostly daily, dispersals and reunions (Goodall, 1986). Their societies, also called groups or communities, typically consist of dependent mother-offspring units, with maturing individuals increasingly engaging in social interactions with non-kin group members. Adult non-kin group members also form long-lasting bonds, which are characterized by preferred spatial associations and grooming interactions (Langergraber et al., 2009; Mitani, 2009). Chimpanzees are thus a highly social species, also known for their cooperative and empathetic nature (e.g., de Waal, 2010; Boesch, 2013), although the specifics and validity of these characterizations are currently under scientific scrutiny.

Secondly, a question of topical relevance: How could the predicted adaptive value of social learning take form in chimpanzees' ordinary lives in the first place? The direct significance of social learning for chimpanzees might become more apparent with a concrete example. Let us envision a context in which chimpanzees are confronted with food-scarcity in their territory. The fruits and plants they normally forage on are for some reason depleted (e.g., think of climatological factors hampering normal vegetation growth). In this particular context, chimpanzees may have to switch to novel sustenance commodities to safeguard their survival, which quite likely involves the acquisition of novel foraging techniques. Now if one particularly innovative individual finds this novel commodity (e.g., a beehive) and invents a technique to extract nutrients from it (e.g., busting the hive with a long stick and scraping the honey out of it with another), then other chimpanzees would obviously benefit from copying this successful individual. Interestingly, this example not only

shows how social learning could be directly relevant for chimpanzees' survival (see Whiten, 2011 for a documented case), it additionally illustrates how certain social learning biases may come about. In this case, it would clearly pay off to copy the behaviour of the successful individual, not just any of the struggling group members. If characteristics like 'success', or, perhaps more indirectly, a 'high prevalence of a certain behaviour' are frequently coupled with a relatively high pay-off compared to individual learning and/or other (social) characteristics, then, given sufficient selection pressures, the conditions would be met for the evolution of social learning strategies (see Laland, 2004).

What do we know about chimpanzees' social learning tendencies and perhaps even cultural expressions? Observational studies have documented many behaviours in chimpanzees' repertoires to be putatively cultural, ranging from tool-use patterns (e.g., nut cracking) to social interactions (e.g., social grooming) (Goodall, 1986; Whiten et al., 1999). Notably, these behaviours have been identified as putatively culture on the basis of the ethnographic method: They seem to be group-specific and not (entirely) explained by genetic or ecological factors. For instance, the grooming hand-clasp was one of the first behaviours to be referred to as possibly cultural (McGrew & Tutin, 1978). Chimpanzees at Mahale mountains would clasp their hands together, raise them up in the air and groom each other with their free hand. Perhaps the most interesting part of this phenomenon was not clear until Dr. Jane Goodall (and subsequently other long-term field workers in other parts of Africa) communicated that she had never seen this social grooming posture at her field-site in Gombe Stream National Park, roughly 100 miles north of the Mahale mountains (see McGrew, 2004). McGrew & Tutin realized that neither genetics nor ecology could explain this group-specificity in chimpanzee behaviour since the chimpanzees at Mahale and Gombe were both from the subspecies *Pan troglodytes schweinfurthii* and the ecological niche they inhabited was practically identical. From this realization, they concluded that the Mahale chimpanzees had somehow invented a new behaviour which had subsequently spread by means of social learning to become a group-specific custom (McGrew & Tutin, 1978; also see McGrew et al., 2001; McGrew, 2004). Similarly, in later years, robust

differences in foraging techniques were observed between wild chimpanzee communities. These particular foraging techniques consisted of methods for ant predation, and because the studied chimpanzees typically used sticks to dip in ant-nests, the behaviour was termed 'ant dipping' (McGrew, 1974). Analogous to the hand-clasp example, chimpanzees from different communities would use different techniques to dip for ants. For instance, while chimpanzees at the Taï forest (Ivory Coast) would use short sticks and eat the ants off of the end of the sticks (Boesch & Boesch, 1990), chimpanzees at Bossou (Guinea) would sweep the sticks covered with ants through their mouths in one go (Sugiyama, 1995). Moreover, the Bossou chimpanzees seemed to use long sticks compared to the sticks used by the Taï chimpanzees, and whereas the Bossou chimpanzees preyed on ants both in their nests and on trails, the Taï chimpanzees have only been observed to dip in ant nests (see McGrew, 1992, also for comparisons with chimpanzees' ant-dipping techniques at Gombe). Although ecological factors like the speed and aggressiveness of the different species of ants that the chimpanzees preyed on seemed to explain some of the variation in ant-dipping techniques, at least part of the variation seemed owing to group-specific customs (Humle & Matsuzawa, 2001; Möbius et al., 2008; Schöning et al., 2008). This conclusion was corroborated by observations on the process of skill acquisition itself (Humle et al., 2009), in similar ways as social learning had been reported for chimpanzees' nut-cracking (Biro et al., 2003) and termite-fishing techniques (Lonsdorf et al., 2004). Moreover, in these tool-use contexts, chimpanzees were not only found in group configurations suggestive of social learning practices (e.g., see Photo 1), but in recent years they have also been observed to engage in complex extraction sequences that would have been difficult to invent for any one chimpanzee individually (e.g., for ant-dipping, see Sanz et al., 2009; for honey extraction, see Boesch et al., 2009; also see Whiten, 2011).



Photo 1. Kirikou, a juvenile chimpanzee in the Tai Forest Ivory Coast, attempts to crack *Coula edulis* nuts while being close to his proficient nut-cracking mother Kinshassa (*Photo courtesy: Mark Linfield and Lydia Luncz*).

By now, many group-specific customs have been identified in chimpanzees (see Whiten et al., 2001), and although some evidence has been found in favour of a more prominent role of genetics in explaining the respective behavioural variation (see Langergraber et al., 2010), scholars seemed to have converged on the idea that social learning underlies at least part of the observed variation (e.g., see Lycett et al., 2010, 2010; Whiten, 2011; Boesch, 2013). Even scholars critical of social learning explanations may now be swayed toward this idea, perhaps especially in the cases where the traditions pertain to social interactions (e.g., grooming hand-clasp and social scratch) for the reason that ecological factors can be more plausibly excluded from their explanation than in the cases where chimpanzees physically manipulate their environment (i.e., in their tool-use behaviours) (also see Nakamura et al., 2000; Laland & Janik, 2006). However, the evidence for chimpanzee culture as identified by the ethnographic method, or more precisely for its pivotal building block *viz.* social learning, remained indirect.

Circumventing the pitfalls of the ethnographic method, comparative psychologists started exploring chimpanzees' cultural potential experimentally (see Mesoudi, 2007; Whiten & Mesoudi, 2008; Caldwell, 2009). Using controlled designs, it became compellingly evident that chimpanzees are indeed fervent social learners, able to create and maintain group-specific traditions consequently (e.g., see Horner et al., 2006; Bonnie et al., 2007; Hopper et al., 2007; Whiten et al., 2007). For instance, the famous 'pan-pipes' challenged captive chimpanzees with a reward-retrieval problem that could be solved in two distinct ways: poking or lifting (see Whiten et al., 2005). Ingeniously, the two techniques, mimicking extractive tool-use behaviour of wild chimpanzees (e.g., ant-dipping and termite fishing), were introduced into two different groups by training one (high-ranking) female on one of the two techniques exclusively. Over time, and after many chimpanzees had observed their group expert solving the task repeatedly, two distinct tool-use traditions emerged on the group level, mirroring the two experts' techniques. The observation that a third group of chimpanzees without any leading example did not converge on one particular technique led the authors to the overall conclusion that "... the 'two alternatives'

methodology [the pan-pipes] shows that learning involves not merely the facilitation of an existing competence, but a capacity to acquire particular local variants of the technique, precisely as required if the behavioural variants identified in wild populations are indeed socially transmitted” (Whiten et al., 2005, p. 738).

Thus, in concert, it seems that the observations from wild populations and the findings of the experimental studies provide substance to the claim that chimpanzees may be a cultural species, with the former showing that chimpanzees might be naturally inclined to copy each other’s behaviour and the latter that chimpanzees possess the very capacity to learn socially, even quite detailed behaviours like tool-use patterns. We have also seen, however, that genetic and ecological factors are important to consider when interpreting group differences. Moreover, additional criteria were proposed for the identification of culture in animal populations, like longevity and continual expansion. As mentioned before, these definitional aspects will be addressed in chapter 2.

Chimpanzees under study

Most of the research presented in this dissertation was conducted at a chimpanzee sanctuary in Zambia called Chimfunshi Wildlife Orphanage Trust (see Photo 2). This sanctuary was founded by David and Sheila Siddle in 1983, when an injured chimpanzee was brought over to their farm. Today, Chimfunshi houses close to a hundred chimpanzees in four woodland enclosures, among the largest in the world. The enclosures have been selected for their close match with chimpanzees’ natural needs (see Ron & McGrew, 1988) and are fenced off by electrified wire. Each enclosure provides a home for one stable group, ranging in size from 12 to 45 chimpanzees. The groups have been formed over time by adding newcomers to existing subgroups until the chimpanzee keepers perceived the groups to be big enough and/or adequately balanced in terms of sex and age, but no chimpanzees have been added to these four (study) groups for at least six years. Since the Chimfunshi chimpanzees have been reproducing at least until 2010, the first formed groups especially consist of expanded families (i.e., these groups have expanded more than the relatively newly formed

groups because they have had more time to reproduce). By now, only half the chimpanzee population at Chimfunshi is wild-born, with the other half thus being sanctuary-born (see chapter 2 for details on the Chimfunshi groups). Owing to the fact that the chimpanzees do not have enough food available in their enclosures to sustain themselves, all chimpanzees are provisioned once a day, from roughly 11:30am till 1:30pm. During this time the chimpanzees are called inside a group-specific holding facility attached to their enclosure, where they receive their food and medical inspection if needed (water is available *ad libitum* inside their enclosures). Apart from this 2-hour period, the chimpanzees remain in their enclosures, also during the night (see Photo 2). Except for a small area where two of the groups are able to see each other, visual contact between the groups is obstructed owing to the distance between the enclosures (the groups may be able to hear each other though). Lastly, the chimpanzees are occasionally confronted with visitors. When visits take place outside regular food-provisioning times, the chimpanzee keepers call over the whole group in the same way as they call the chimpanzees for daily provisioning and give the chimpanzees treats like sugarcane and biscuits. These visits typically last 10-15 minutes, during which no research is conducted (with an extra delay of 30 minutes after the visitors have left the premises to minimize any potential carry-over effects from visit-induced behaviour into our observations).

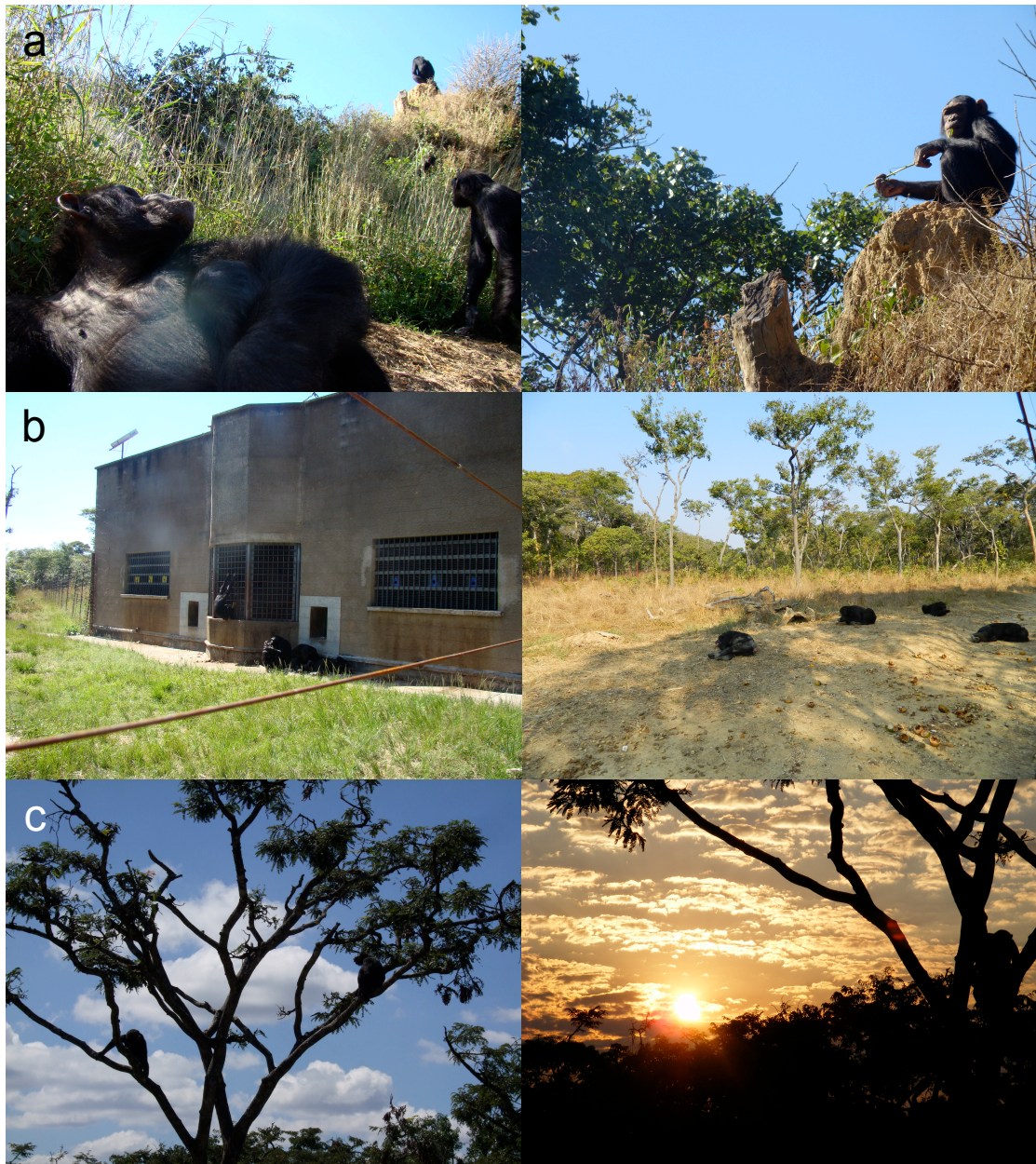


Photo 2. Chimfunshi Wildlife Orphanage Trust, where (a) the chimpanzees live in Miombo woodlands which provide natural resources like edible plants and (branches to fish for) termites; (b) natural experiments can be conducted in which the chimpanzees can partake (left: yellow and blue ‘exchange stations’ on the handling facility. Some chimpanzees were trained to put tokens through these stations in exchange for a food reward; the critical test was whether the untrained chimpanzees would learn this skill and if so, if they would favour the station where most of their group members exchanged tokens – *unpublished data*), or enjoy the spacious enclosures ranging from 20 to 75 hectares instead (green and lush (left) or yellow and dry (right) dependent on the season); (c) the chimpanzees make nests and spend their nights outside in the woods.

Another part of the research was conducted at the Wolfgang Köhler Primate Research Center in Leipzig, Germany. Although the chimpanzees at the WKPRC live in a less-typical chimpanzee environment than the Chimfunshi chimpanzees, they are looked after with great care by both the WKPRC and Leipzig Zoo. For instance, they are housed in a relatively large enclosure compared to other zoos, with many enriching features like puzzle-boxes, climbing structures, natural vegetation and running water. As such, the chimpanzees are healthy and display much species-typical behaviour, with only minor occurrences of stereo-typical behaviour (i.e., repetitive behaviour which may be indicative of stress). Most of them are also highly motivated to take part in behavioural studies, which are being conducted every day from 8am-12pm (4 hours). The great advantage of studying the WKPRC chimpanzees is the possibility to create highly controlled study-settings, i.e., settings where confounding factors can be eliminated. For instance, in contrast to the options at Chimfunshi, chimpanzees at the WKPRC can be tested in isolation from their group, or with only one pre-determined partner (e.g., see chapter 7). This possibility thus allows for obtaining scientifically powerful data. However, compared to the chimpanzees at Chimfunshi, studying the WKPRC chimpanzees does not yield data with a high degree of ecological validity. In contrast to the WKPRC chimpanzees, before the onset of the research described in this dissertation the Chimfunshi chimpanzees had never been studied, except for a few observational projects. Thus, from the perspective of their experiences with research, one could argue that results from studying the Chimfunshi chimpanzees reflect close to natural behaviour. On the other hand, many of the wild-born chimpanzees at Chimfunshi have suffered physical and psychological trauma before they arrived at the sanctuary. While consensus exists between the involved people at the sanctuary regarding the relative health of the chimpanzees, based on face-value (e.g., the perceived absence of stress indicators like excessive self-grooming and stereo-typical behaviour), the effects of these early traumas remains to be thoroughly assessed. Overall, studying the Chimfunshi and WKPRC chimpanzees provides a powerful opportunity to learn about our closest living relatives. However, from a scientific point of view, it

should be noted that the studied chimpanzees are not faced with the same socio-ecological pressures as their wild counterparts, and that the results presented here should be interpreted in light of this consideration.

Thesis outline

The main goals of this thesis are to validate whether socially-learned group differences exist among chimpanzees, whether their social learning proclivities may be guided by the conformity bias which has been identified as a driving mechanism behind the emergence of between-group variation, whether chimpanzees are equally poised toward social information as a culturally-rich species like humans, and how any of these findings would relate to the (ethological) concept of culture. Throughout the dissertation, these goals will be pursued such that many chapters will address several of them in conjunction. More specifically, this thesis addresses the following questions:

Question 1: Are there behaviours among chimpanzees that could be identified as culture?

In the context of the ‘animal cultures debate’, in this study, we aimed to scrutinize one particular behaviour that has been identified as ‘putative cultural’ in previous research: the grooming hand-clasp (McGrew & Tutin, 1978; Whiten et al., 1999). First documented in the chimpanzees living on the Tanzanian Mahale mountains (McGrew & Tutin, 1978), the grooming hand-clasp (GHC) refers to a peculiar social behaviour in which two individuals extend one arm overhead and clasp each other's upraised hands while they groom each other with the other arm (see Figure 1 and 2 in chapter 2). The GHC was tentatively advocated as a ‘social custom’, akin to human traditions, when a well-studied nearby group of chimpanzees (Gombe Stream, Tanzania: see Goodall, 1986) was not observed to engage in the GHC (McGrew & Tutin, 1978; McGrew, 2004). The reasoning behind this argumentation was that if GHC had been a species-typical or ecologically-induced behaviour, then both the chimpanzees at Mahale and

Gombe would have had GHC in their behavioural repertoire. Since only the chimpanzees at Mahale engaged in GHC, it seemed sound to conclude that it had to be a *socially transmitted custom*.

However, over time, an increasing number of chimpanzee populations have been observed to engage in the GHC (Webster et al., 2009), indicating that GHC behaviour might be species-typical grooming behaviour after all. In light of this new development, the original assertion that GHC represents a social custom needs to be revisited as subtle ecological differences between the groups at Mahale and Gombe (e.g., low-hanging branches that chimpanzees use to hold onto while being groomed underneath their armpit) could have triggered the GHC behaviour in one but not the other community. Therefore, in chapter 2, I set out to investigate not which groups of chimpanzees engage in GHC and which groups do not, but whether the groups that do engage in GHC prefer different styles. Moreover, I explore to what extent GHC behaviour satisfies current definitions of ‘culture’ by analysing GHC-style *variation* across groups, the *longevity* of the GHC behaviour and the horizontal (within-generation) and vertical (between-generation) *expansion* of GHC behaviour (Perry et al., 2003; Whiten, 2003). Furthermore, arm-length differentials between clasping partners are scrutinized for they may contribute substantially to the postural style of the GHC dyads. These aspects were investigated in the Chimfunshi setting where genetics and ecology can be assumed to play merely a peripheral role in explaining group differences, especially in case of behavioural style-differences (as opposed to coarse absent / present characterizations). By way of preview, results reveal that i) while only two of the four Chimfunshi chimpanzee communities engage in GHC behaviour, stable style differences exist between the two GHC communities in terms of preferred clasping points (‘palm-palm’ vs. ‘wrist-wrist’), ii) the GHC behaviour has been part of their behavioural repertoires for at least 5 years, and iii) the GHC behaviour has transmitted both to a substantial part of the within-generation group members and to the majority of next-generation chimpanzees. Moreover, since arm-length differentials do not contribute to the prediction of GHC styles, we tentatively conclude that the GHC behaviour in the Chimfunshi chimpanzees is at least partly cultural.

Question 2: Do chimpanzees spontaneously copy arbitrary behaviour?

In chapter 2, we show that neighbouring groups of chimpanzees can be characterized by different styles of social grooming behaviour and that these differences are likely due to social learning processes. However, it remains unaddressed whether chimpanzees would also adopt each other's behaviour when the target behaviour is not part of the typical behavioural repertoire of chimpanzees (cf. social grooming). This question is interesting to address as many human forms of culture contain arbitrary elements (e.g., fashion fads: see Laland et al., 2011), whereas most, if not all, putatively cultural behaviours of chimpanzees relate to physical and/or social necessities, like foraging and grooming (see Whiten et al., 1999; Luncz et al., 2012; van Leeuwen et al., 2012; cf. Hobaiter & Byrne, 2010). Thus, in chapter 3, I set out to find an arbitrary idiosyncratic behaviour among the Chimfunshi chimpanzees and investigate whether group members would copy this behaviour. Fortuitously, during an early fieldtrip, a behavioural pattern was observed that met the inclusion criteria. One adult female chimpanzee would select a stiff, straw-like blade of grass, insert the grass into one of her own ears, adjust the position, and then leave it in her ear during subsequent activities. This 'grass-in-ear behaviour' (henceforth 'GIEB') was unique to this one inventor chimpanzee and had no discernable purpose, which made it a good test-case for studying the emergence of arbitrary fads. Over the course of one year, the GIEB was adopted and frequently displayed by 8 out of 12 group members, while it was observed only once across the three neighbouring groups of chimpanzees. In almost all cases, the copy-cats engaged in GIEB only in the presence of the inventor displaying the GIEB. When the inventor died in 2013, the small body of available records showed that at least 2 group members persisted in GIEB. Overall, we interpret these findings as reflecting chimpanzees' intrinsic motivation to copy each other's behaviour, tentatively define the underlying learning mechanism in terms of response facilitation, and relate the arbitrariness of the copied behaviour and the fact that it outlasts its originator to human cultural phenomena.

Question 3: Can conformity be pivotal to the emergence of cultural group differences in chimpanzees? An appraisal of current evidence.

Conformity to the majority of group members accentuates group differences by facilitating within-group homogeneity and between-group heterogeneity (Boyd & Richerson, 1985; Henrich & Boyd, 1998). In a slightly different form (see chapter 6), conformity has been documented as a robust human characteristic (Asch, 1955, 1956; also see Claidière & Whiten, 2012). With the aim to identify evolutionary precursors of this human characteristic, conformity has been experimentally addressed in chimpanzees (Whiten et al., 2005; Bonnie et al., 2007; Hopper et al., 2011) and capuchin monkeys (Dindo et al., 2008; Dindo et al., 2009; Perry, 2009). The importance of finding conformity in chimpanzees might not only lie in its potential to shed evolutionary light on human conformity, but also in its power to explain the emergence of cultural group differences in chimpanzees like the ones assessed in chapter 2 and 3 (grooming hand-clasp and grass-in-ear behaviour, respectively). However, where research specifically designed to investigate conformity in chimpanzees has advocated positive evidence (Whiten et al., 2005; Hopper et al., 2011), methodological obstacles cloud the soundness of their conclusions. In chapter 4 I therefore scrutinize the methodological features of all studies that have claimed to find evidence of conformity in nonhuman primates. Focusing on the most crucial methodological aspects, we defend the alternative explanation that the primates in the respective studies did not match the majority strategy according to conformity principles (e.g., see Sherif, 1936; Asch, 1956), but rather as a consequence of their evidenced tendency to prefer familiar over non-familiar strategies, which has been labelled as ‘conservatism’ (Marshall-Pescini & Whiten, 2008; Hrubesch et al., 2009) or ‘habit formation’ (Pesendorfer et al., 2009). Furthermore, we find that conformity studies have typically used inconspicuous ways to demarcate the minority from the majority strategy (i.e., the use of two small yet different tokens) and assumed rather than tested whether the minority individuals had actually observed a conflicting majority strategy at the time they were tested. In conjunction, these methodological considerations lead to the conclusion that conformity has not yet been tested adequately in nonhuman

primates and thus that the jury is still out on the questions of whether human conformity may be a derived trait and whether conformity could possibly govern the emergence of cultural group differences in nonhuman primates.

Question 4: Do chimpanzees flexibly adjust their familiar behaviour to conform to the majority (or to obtain more rewards)?

In chapter 5, we aim to incorporate the methodological improvements suggested in chapter 4 into empirical studies. More specifically, we design empirical studies such that the confounding effect of ‘persisting in familiar strategies’ (a form of ‘conservatism’: see chapter 4) could be circumvented. This is achieved by training a minority and a majority separately on two distinct but equally effective food-yielding actions prior to the test phase during which the whole group is reunited and given the opportunity to use either action (Study 1a: tokens, Study 1b: locations). Contrary to previous studies, this design allows for conclusions on conformity while controlling for conservative tendencies. Importantly, this design also taps into conformity more validly than the previous studies as conformity has traditionally been operationalized as the tendency to *forgo* instead of persisting in familiar behaviour (e.g., Sherif, 1936; Asch, 1956; Bond, 2005). Moreover, our design encompasses two additional features that may be considered improvements on previous research: i) the usage of conspicuously different actions for the minority and the majority, which increases the likelihood that chimpanzees perceive the difference between the two sub-groups, and ii) the verification that chimpanzees in the minority actually pay attention to the majority of their group members engaging in the alternative action, which is essential for a valid interpretation of the behavioural patterns in terms of conformity. Finally, by testing our design in two independent chimpanzee populations (Leipzig Zoo and Chimfunshi) and including a condition in which the profitability of one strategy increases 5-fold compared to the other strategy, the findings become more generalizable and interpretable, respectively. Upon confirming that the minority chimpanzees paid sufficient attention to the conflicting action being performed by the majority of group members, results show that chimpanzees do not conform their behaviour to the majority.

Conversely, chimpanzees readily switch their strategies when one strategy is upgraded in profitability, thereby maximizing their gains. These findings indicate that although chimpanzees can flexibly switch strategies, they are less inclined to do so following conformity principles than reward-maximizing heuristics.

Question 5: Has conformity been operationalized congruently across disciplines and how can we improve its study?

Where chapter 4 and 5 focus on conformity in nonhuman primates and advocate the stance that conformity needs scrutiny on a more detailed level, chapter 6 addresses conformity operationalizations across taxa and advances the idea that majority influences should be demarcated from social influences for similar reasons of empirical accuracy. Specifically, in chapter 6, we explore the extent to which the evidence for conformity in humans and nonhuman animals may alternatively be explained by the animals' preference for social information regardless of the number of individuals demonstrating the respective behaviour. With this aim in mind, firstly, studies on apes (including humans), monkeys, rats, fish, birds and (social) insects are reviewed. We distinguish between the conformity definition that emerged from the study of cultural evolution (Boyd & Richerson, 1985; Henrich & Boyd, 1998) and human social psychology (Jenness, 1932; Sherif, 1936; Asch, 1951), and interpret the reviewed evidence in light of the latter for the reason that the former operationalization has only been tested empirically a few times (Pike & Laland, 2010; Morgan et al., 2011; Claidière et al., 2012), while studies claiming to have found evidence in sense of the latter operationalization are relatively abundant (see chapter 6). Moreover, the human psychology operationalization allows for a better integration of conformity in the study of behavioural decision-making trade-offs than the cultural evolutionary variant, as the former but not the latter contains the psychologically and decision-making relevant aspect of 'forgoing old and adopting new behaviour'. Our review addresses instances where the empirical designs have not been sufficiently precise to control for social influences independent of majority influence and finds that some 'conformity' studies have not even incorporated a majority manipulation in their designs. It is therefore concluded that in order to

compare conformity findings, definitional and methodological calibration is needed. Secondly, building on earlier conformity work (Asch, 1956; Starkweather, 1970), we argue for the integration of a measure that takes into account the magnitude of the focal subject's persistence in his individual behaviour and the extent to which the behaviour demonstrated by the majority deviates from the subject's behaviour. For instance, one might argue that individuals adopting an equally effective alternative strategy (e.g., the chimpanzees in Whiten et al., 2005) conform less markedly than individuals adopting an ineffective alternative (e.g., the human adults in Asch, 1956).

Question 6: Do children and chimpanzees place similar value on social information?

Chapter 7 empirically addresses a more fundamental question sparked from the theoretical study of majority and social influences on animals' decision-making in chapter 6. The following question seeks an answer for the striking panthropological conclusion that although cultural expressions are found in *Pan* species, human cultural proliferation by far exceeds the cultural proliferation of chimpanzees (Whiten et al., 2003; Richerson & Boyd, 2005; Mesoudi, 2011).

In general, animals might be expected to rely on individual over social information. Environmental parameters like predation risk or unpredictability could bias animals toward preferring one information source over the other, but in the absence of moderating variables, animals including humans will likely rely on individual information by default (Laland, 2004; Eriksson & Strimling, 2009; Kendal et al., 2009). Species differences in relative individual and social information reliance, however, are expected based on ecological and systemic variation (Wallace, 1858; Darwin, 1859; Bergman, 2006) and have indeed been observed between for instance stickleback species (Coolen et al., 2003). Besides yielding information on species-specific decision-making strategies, since the diffusion of information is inherently linked to relative within-group homogeneity compared to between-group-heterogeneity, insights in individual and social information weighing could also shed light on species potential to develop behavioural traditions akin to the ones addressed in chapter 2 and 3.

Therefore, in chapter 7, we aim to contribute to our understanding of the cultural gap between humans and chimpanzees by exploring the following research question: Do humans and chimpanzees place similar value on social information?

Summary

This thesis seeks to explore the extent to which chimpanzees organize their social lives by means of social learning processes that are pivotal to our definition of culture. In pursuit of this quest, observational and experimental methods are used to study captive and semi-captive groups of chimpanzees. Chapter 2 and 3 chart behavioural differences between four neighbouring groups of chimpanzees in light of cultural diversity. Both functional (chapter 2) and non-functional (chapter 3) behaviours are examined. Chapter 4 and 5 investigate whether cultural differences between chimpanzee communities can be explained by conformity to majorities. Existing evidence of conformity in chimpanzees is methodologically evaluated (chapter 4) and empirically revisited (chapter 5). Finally, the focus is broadened by exploring the validity of conformity claims in general, proposing to integrate conformity in the intricate network of (social) learning biases (chapter 6), and by empirically testing the hypothesis that the difference in cultural proliferation between humans and chimpanzees could be due to their differential reliance on social information (chapter 7).

Neighbouring chimpanzee communities show different preferences in social grooming behaviour

Chapter 2

Based on:

Van Leeuwen, E. J. C., Cronin, K. A., Haun, D. B. M., Mundry, R. & Bodamer, M. D. (2012). Neighbouring chimpanzee communities show different preferences in social grooming behaviour. *Proceedings of the Royal Society B: Biological Sciences*, 279(1746), 4362-4367.

Abstract

Grooming hand-clasp (GHC) behaviour was originally advocated as the first evidence of social culture in chimpanzees owing to the finding that some populations engaged in the behaviour and others do not. To date, however, the validity of this claim and the extent to which this social behaviour varies between groups is unclear. Here, we measured (i) *variation*, (ii) *durability*, and (iii) *expansion* of the GHC behaviour in four chimpanzee communities that do not systematically differ in their genetic backgrounds and live in similar ecological environments. Ninety chimpanzees were studied for a total of 1029 hours; 1394 GHC bouts were observed between 2010 and 2012. Critically, GHC style (defined by points of bodily contact) could be systematically linked to the chimpanzee's group identity, showed temporal consistency both within- and between-groups, and could not be accounted for by the arm-length differential between partners. GHC has been part of the behavioural repertoire of the chimpanzees under study for more than nine years (surpassing *durability* criterion) and spread across generations (surpassing *expansion* criterion). These results strongly indicate that chimpanzees' social behaviour is not only motivated by innate predispositions and individual inclinations, but may also be partly cultural in nature.

Introduction

Grooming hand-clasp (GHC) behaviour was the first social behaviour to be described as a 'social custom' in chimpanzees (McGrew & Tutin, 1978). This claim was based on the observation that the chimpanzees of the K(ajabala)-group in the Tanzanian Mahale mountains engaged in a peculiar social behaviour in which two individuals extend one arm overhead and clasp each other's upraised hands while grooming each other with the other arm, while the well-studied chimpanzees of the nearby Gombe field site were never observed engaging in it (McGrew & Tutin, 1978). In their influential paper, McGrew and Tutin elaborate on the importance of this finding by arguing that this present/absent distinction can neither be explained by genetic predispositions nor by environmental factors. This line of reasoning led the authors to conclude that the GHC behaviour contains the necessary prerequisites for it to be considered 'cultural' (McGrew & Tutin, 1978).

While McGrew and Tutin's arguments have been adopted by later researchers investigating GHC behaviour in chimpanzees (de Waal & Seres, 1997; Nakamura & Uehara, 2004; Bonnie & de Waal, 2006; Humle et al., 2009), the core question of whether this particular social behaviour can be validly considered 'cultural' has escaped closer empirical scrutiny. We support the view that a detailed look at the behavioural differences between groups beyond a mere present/absent distinction is necessary to reveal a species' capacity and tendency to adopt a group-specific behavioural variant (Perry et al., 2003; Nakamura & Uehara, 2004; Whiten & van Schaik, 2007). This may be especially relevant in the case of GHC behaviour, with its current prevalence and similarity to innate predispositions: i) since the late seventies, GHC behaviour has been observed in at least 16 independent populations to date (Webster et al., 2009), and ii) GHC behaviour closely resembles chimpanzees' natural tendency to mutually groom with arms clasped onto overarching branches and initiate grooming bouts with upraised arms (Goodall, 1968; McGrew & Tutin, 1978). Since these two observations seem to point more towards a genetic and/or ecological explanation, it seems essential to investigate further whether there are any systematic differences in the GHC behaviour between groups above and beyond those that can be accounted for by differences in ecological and genetic

differences. The crucial focus of the investigation would thus be the different execution of this social behaviour, not only whether some populations have added to their repertoire the clasping of hands, while others have not. Accordingly, here, we scrutinized *variation* in GHC style between four communities of chimpanzees that have not been part of the hand-clasp literature yet and provide the largest dataset of hand-clasp bouts analysed to date. Additionally, and partly expanding the ethological concept of culture (chapter 1), we applied four criteria to assess whether GHC behaviour could be considered cultural in a conservative sense (Perry et al., 2003; Whiten, 2003): *durability* (lasting for at least 6 months), *expansion* (increasing number of performers over time), and the exclusion of *genetic* and *environmental* determinants.

To our knowledge, the studies by McGrew et al. (2001) and Nakamura & Uehara (2004) are the only investigations that systematically assessed the variance in GHC styles beyond the present/absent distinction. Building on the work of McGrew et al. (2001), Nakamura & Uehara (2004) investigated whether particular GHC styles could be reliably associated with either of the two communities under study: the K(ajabala)- and M(imekire)-group in the Mahale mountains, Tanzania. After analysing individual and group preferences based on 'palm-contact' and the angles in which both the wrist and elbow of the clasping arm were flexed, they provisionally concluded that 'palm-to-palm' contact and the straight wrist during GHC bouts were signatures of the K-group, while the M-group used 'palm-to-palm' contact only very infrequently and was better characterized by the use of flexed wrists during hand-clasp grooming (Nakamura & Uehara, 2004). While these studies provided preliminary evidence that GHC behaviour might be (partly) cultural in nature, the conclusions were based on occurrences rather than individuals and a relatively limited sample size (McGrew et al., 2001; Nakamura & Uehara, 2004).

The aim of this study was to evaluate the amount of group-level variation that characterizes GHC behaviour in chimpanzees, using a large number of observations and testing whether the behaviour is durable, expanding, and varies between groups independent of genetic and environmental determinants (Perry et al., 2003; Whiten, 2003). In pursuit of this aim, we first systematically observed all study groups to establish an initial GHC present/absent distinction.

Second, we analysed whether there were any differences in the GHC styles between the groups that engaged in the GHC behaviour and assessed whether the variation was consistent over time. Third, we determined when the GHC entered the behavioural repertoires of the groups under study and investigated whether formerly naive individuals started hand-clasping by comparing the active dyads between 2007, 2010 and 2011. Finally, to investigate whether GHC styles were systematically influenced by physical properties, we measured the arm-length differential between GHC partners. Because chimpanzees typically engage in GHC behaviour with stretched arms, variation in arm length could possibly generate variation in the GHC style that is defined by the points of arm-contact (see *Methods*). We studied four semi-wild groups of chimpanzees that are socially isolated from one another, yet live in the same forest at the Chimfunshi Wildlife Orphanage Trust in Zambia (see chapter 1). The individuals at CWOT that were born in the wild were likely taken from their wild social group while infants, as is the case for most rescued sanctuary chimpanzees. Given that the youngest age at which GHC has been observed is 5 years and 9 months (Bonnie & de Waal, 2006), it is a safe assumption that these individuals had no experience engaging in GHC behaviour prior to their arrival at CWOT, thus minimizing the potential carry-over effects of early experiences in the wild. Moreover, since CWOT accepted chimpanzees from all over Africa and the groups were formed based on the dates of the chimpanzees' arrivals (S. Siddle & I. Mulenga, pers.comm.), the chimpanzee communities under study do not differ systematically in their genetic backgrounds. In conjunction, these factors deem any observed differences between groups unlikely to be due to genetic or ecological influences.

Methods

Subjects and field-site

Subjects were 90 chimpanzees in four stable social groups (see Table 1 for details on years of formation, sex distribution, age, and number of GHC subjects).

Table 1. Demographic details on the chimpanzee group at the Chimfunshi Wildlife Orphanage Trust at the start of the study (May 2010), and the number of individuals that engaged in the GHC behaviour throughout the observation window of this study. The number of adults and non-adults is shown in parentheses (adult.non-adult), where “adult” corresponds to 12 years and older.

	<i>Group 1</i>	<i>Group 2</i>	<i>Group 3</i>	<i>Group 4</i>
Years of formation	1984-1989	1990-1994	1995-1999	2000-2002
Males	12 (5.7)	11 (3.8)	6 (4.2)	8 (6.2)
Females	11 (7.4)	29 (17.12)	7 (6.1)	5 (5.0)
Mean age (years)	16	14	13	12
Age range (years)	2-29	2-33	0-25	2-19
# of ghc individuals 2010	18	30	0	0
# of ghc individuals 2011	15	33	4	0

The chimpanzees live under semi-wild conditions at the Chimfunshi Wildlife Orphanage Trust, a sanctuary in the north-western part of Zambia (see chapter 1). Approximately half the chimpanzees were wild-born, the other half were mother-reared at the CWOT. The enclosures consist of fenced Miombo forest and range in size from 20-80 hectares. Except for a few meters along the fence line between group 3 and 4, the chimpanzees in the different groups cannot see each other. Three chimpanzees that are currently housed separately in group 1 and 2 shared group membership during the initial group-formation process (in 1990).

Data collection procedure

Data were collected through all-occurrence sampling (Martin & Bateson, 2007), in which subjects were identified individually. Observation sessions took place for 10 days between May-July 2010 and 10 days between May-July 2011, from 8:00am to 11:45am. This time window was chosen because the chimpanzees tend to spend their time relatively close (binocular view distance) to the indoor holding spaces prior to mid-day feeding, thus increasing observation opportunities. In 2010, these observations were completed for all four groups, yielding a total of 150 hours (37.5 hours per group). In 2011, this methodology was repeated for the two groups that were known to engage in the GHC behaviour, yielding a total of 75 hours of observation (37.5 hours per group). During the observation sessions, all visible GHC bouts were both live

coded and video-recorded from an observation deck on top of the indoor facilities by three observers who recorded the identity and hand-clasp style. Binoculars were used. If identity and style could not be determined from live observation or video, the event was counted for overall frequency but excluded from other analyses. Reliability between the lead observers of group 1 and 2 was further established by independently scoring 112 GHC styles from a random selection of videos (Cohen's $K=0.91$) (Cohen, 1960).

In addition to the observation sessions, we used focal follows to investigate GHC behaviour in the Chimfunshi chimpanzees. Focal follow sampling (Martin & Bateson, 2007) started in February 2011 and has yielded 804 hours of observation through March 2012 (group 1–4: 218, 200, 173 and 213 hours, respectively). Our focal follow method is comprised of daily observations of each group between 8:30-11:00 and 14:30-17:00. Focal subjects were selected through systematic, randomized sampling of the chimpanzees' entire enclosure (as seen from the fence line) and chimpanzees were video-recorded for 10 consecutive minutes. During the review process of the focal follow videos, the hand-clasps by the focal individual or any other individual in view were extracted. The GHC bouts from these videos were analysed and reported separately (see *Results*).

Additional data were obtained from records from May-August 2007 (41 days of all-occurrence sampling in both group 1 and 2, minimally 240 hours per group). However, since these data were not collected with the same methodology as in 2010 and 2011, only information on the identities of the GHC partners was extracted from this dataset in order to investigate the transmission of GHC behaviour over time.

Grooming Hand-Clasp operationalization

McGrew & Tutin (1978) operationalized the Grooming Hand-Clasp as 'a symmetrical postural configuration in which two participants extend an arm overhead and then either one clasps the other's wrist or hand, or both clasp each other's hand. Meanwhile, the other hand engages in social grooming of the other individual's underarm area revealed by the upraised limb, using typical finger movements' (McGrew & Tutin, 1978). We extended their operationalization by

including two more individually scored clasping styles based on the part of the arm or hand that makes contact with the partner, generating the categories: palm, wrist, forearm and other. Almost all possible combinations of these individual styles were observed at least once across groups (see Table 2).

Table 2. Frequencies of GHC styles during observation sessions across groups and years (in bouts).

<i>Group</i>	<i>1</i>		<i>2</i>	
<i>Year</i>	<i>2010</i>	<i>2011</i>	<i>2010</i>	<i>2011</i>
forearm forearm	1	0	4	0
forearm palm	2	3	2	6
forearm wrist	0	3	4	5
other other	11	1	6	1
other palm	1	0	3	0
other wrist	0	0	2	0
palm palm	75	48	252	238
palm wrist	15	14	29	19
wrist wrist	19	22	12	13

The category 'other' included styles that could not be reliably classified as either palm, wrist or forearm, but were too diffuse to form one distinct category (e.g., elbow, upper arm). A GHC bout was defined by two individuals making bodily contact by means of one of the above-mentioned GHC styles, ending with the release and lowering of the arms (see Figures 1 and 2 for examples).



Figure 1. Grooming hand-clasp example: the chimpanzees use the 'palm-to-palm' style



Figure 2. Grooming hand-clasp example: the chimpanzees use the 'wrist-to-wrist' style

Analyses

To test whether frequencies of different GHC styles differed between groups, we used a Generalized Linear Mixed Model (GLMM; Baayen, 2008). GLMMs allow for determining the effects of one or more predictor variables on a response variable while at the same time accounting for non-independence of the response variable due to repeated observations (of, e.g., the same individuals or dyads). In the models, we included group as a fixed effect, and dyad and the two interacting individuals as random effects. To account for potential daily variation in the frequencies of GHC styles, we included day as a further random effect. Furthermore, we included the year and the interaction between group and year as fixed effects into the model in order to test whether group differences were stable over time. Finally, in the models exploring group differences in GHC style, we only included dyads that engaged in the GHC behaviour at least five times for the reason that an investigation of relative preferences necessitates repeated measures within the same dyad. As the binary response, we first chose the most commonly expressed symmetrical GHC style ('palm-to-palm'; Figure 1) as opposed to any other style. In a second model, we additionally investigated the expression of the second most commonly expressed symmetrical GHC style ('wrist-to-wrist'; Figure 2).

A separate model tested whether the GHC style symmetry was influenced by the arm-length differential between the clasping partners. Measures of arm lengths were obtained for 27 subjects by photographing chimpanzees reaching for a 30cm piece of sugar cane through the bars of their indoor holding space and assessing arm length digitally. Inter-observer reliability was established by a second individual independently scoring 100% of the available photos (Pearson correlation: $R=0.97$, $N=76$). This model contained the same random effects as the previous models, but included neither year nor the interaction between group and year, and dyads were included even if they had engaged in fewer than five hand-clasp bouts. Moreover, the response variable comprised the symmetry vs. a-symmetry of the dyadic GHC style (e.g., palm-to-palm=symmetrical; palm-to-wrist=a-symmetrical). Crucially, the model included the absolute difference between the arm lengths of the two partners as a fixed effect.

Since the assignment of the two grooming individuals to the two random effects was completely arbitrary, in all models, we randomized this assignment 1,000 times and averaged the results of the corresponding 1,000 GLMMs. GLMMs were implemented in R (Team, 2011) using the function `lmer` of the R package `lme4` (Bates et al., 2011) with binomial error structure and logit link function.

For the analyses on the expansion of the GHC behaviour, we focused on all juveniles that reached the age of the youngest chimpanzee that has been reported to engage in the GHC behaviour (5 years and 9 months, Bonnie & de Waal, 2006) during our data collection (2007-2011).

Results

Variation in GHC style

Two of the four study groups were observed to engage in the GHC behaviour during the observation sessions in 2010 and 2011 (group 1 and 2); no GHC bouts were observed in the other two groups (group 3 and 4). Overall rates of GHC bouts in group 1 and 2 during the observation sessions were 4.7 bouts/hour (n=163) and 11.7 bouts/hour (n=410) in 2010, and 1.7 bouts/hour (n=61) and 15.4 bouts/hour (n=538) in 2011, respectively. In 811 of the 1172 observed GHC bouts, we were able to identify GHC style for both partners (see Table 2).

Crucially, there were marked group differences in the frequencies with which the palm-to-palm and wrist-to-wrist styles were used (see Figure 3).

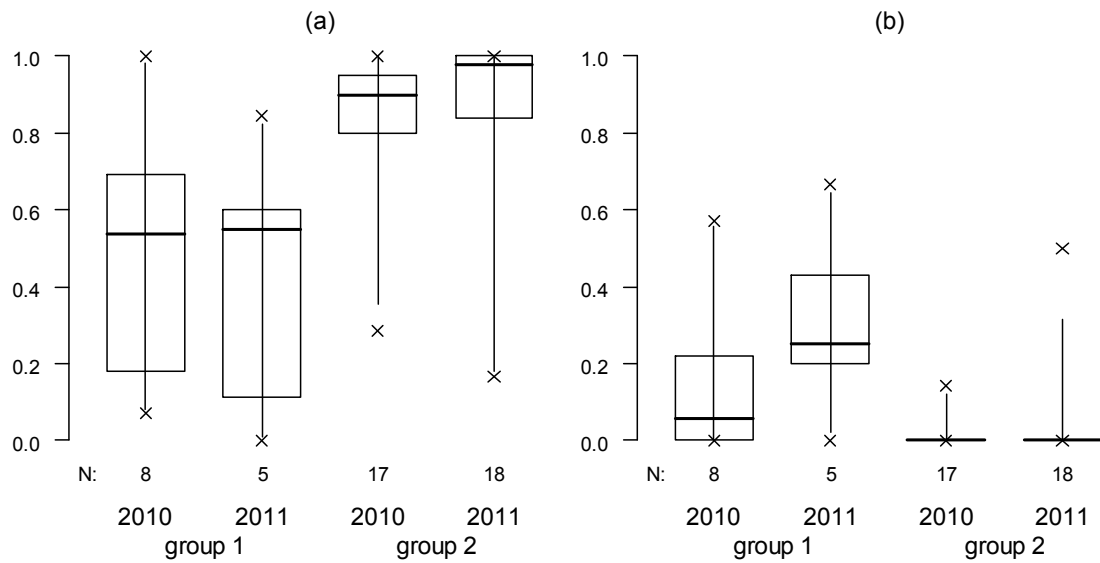


Figure 3. Proportion by which palm-to-palm (a) and wrist-to-wrist (b) were used, separately per year and group. N refers to the number of dyads (only dyads with at least five GHC bouts included). Sample sizes for this analysis were 619 GHC bouts and 42 subjects. Shown are medians (thick horizontal lines), quartiles (boxes), percentiles (2.5 and 97.5%, vertical lines) and minimum and maximum (laying crosses) of the proportions per dyad.

The palm-to-palm style was significantly more frequent in group 2 ($p=0.008$, $B=1.86$, $SE=0.70$, $N=619$), while the wrist-to-wrist style was significantly more frequent in group 1 ($p=0.015$, $B=-3.05$, $SE=1.25$, $N=619$; both tests derived from models not comprising the interaction, see below). The interaction between year and group was not significant in the wrist-to-wrist model ($p=0.763$, $B=-0.72$, $SE=2.35$, $z=-0.30$) but tended to be so in the palm-to-palm model ($p=0.069$, $B=1.36$, $SE=0.74$, $z=1.83$). Inspection of the results suggested that the group differences did not change strongly over the course of 2010-2011 (see Figure 3).

Another 59 GHC bouts for group 1 and 160 GHC bouts for group 2 were observed during focal follow sampling. We were able to identify the GHC styles for both partners in 53 cases involving 17 subjects in group 1 and 143 cases involving 31 subjects in group 2. The focal follow data revealed the same pattern as the data collected during the observation sessions in 2010 and 2011. The percentage of GHC bouts that was palm-to-palm in group 2 was higher than in group 1 (group 2: 90.2%; group 1: 13.2%). The percentage of GHC bouts that was wrist-to-wrist was greater in group 1 than in group 2 (group 1: 49.1%; group 2:

1.4%). While no GHC bouts have been observed in group 3 since the formation of this group in 1995, 4 individuals in this group were observed to engage in GHC behaviour during the focal follow period, resulting in 3 bouts in total (first bout in September 2011). Given the low frequency of occurrence, however, the GHC behaviour in group 3 was not subject to analysis. Notably, group 4 was never observed to engage in GHC behaviour, not during the observation sessions, nor during the focal follow period.

Influence of arm-length differential on GHC style

The symmetry of the dyadic hand-clasp styles was not predicted by the absolute arm-length differential of the clasping partners ($p=0.61$, $N=321$ GHC bouts, 27 subjects; 53 dyads).

Durability of the GHC behaviour

Based on personal observations and communication with the chimpanzee keepers, we can conservatively state that the GHC behaviour has been part of the behavioural repertoire of the Chimfunshi chimpanzees in groups 1 and 2 for at least 9 years (M. Bodamer, pers. obs.).

Expansion of the GHC behaviour

The assessment of the GHC transmission showed that 20 juveniles (11 females) out of the 23 juveniles in the hand-clasp groups (11 females) started engaging in the GHC behaviour and that in 83% of the possible cases the mother was the first partner of these new hand-claspers (see Table 3).

Table 3. Expansion of the GHC behaviour in the chimpanzee groups at Chimfunshi that engaged in the GHC behaviour throughout 2007-2011. Information on all juvenile chimpanzees that reached at least the age of 5 in 2011 is displayed (YOB = year of birth; Empty cell = no GHC behaviour observed; GHC partner in writing = kin; GHC partner in number = non-kin).

	<i>Sex</i>	<i>YOB</i>	<i>2007</i>	<i>2010</i>	<i>2011</i>
Group 1					
Bob	♂	2001	Mother + 2	Mother + 1	
Gerard	♂	2002	Mother	Mother	Mother + 1
Ilse	♀	2002	Mother	Mother	Mother
Brandon	♂	2006			
Regina	♀	2006		Mother	Mother
Rusty	♂	2006			Mother
Group 2					
David	♂	2001	Mother + 1	Mother + 1	2
Debbie	♀	2001	Mother	Mother + 5	Mother + 2
LJ	♂	2001		Sister + 1	Mother + sister + 4
Marc*	♂	2001	Mother		
Maxine&	♀	2001	Mother + 1	Mother + 1	Mother + 2
Thomas~*	♂	2001	3		
Tilly^	♀	2001	Mother	Mother + 3	Mother + sister + 3
Claire	♀	2002		Mother	Mother + sister + 1
Vis	♂	2002		-	1
Doug	♂	2003	Mother	Mother + sister	Mother + sister + 1
Nina	♀	2003	Mother	Mother + sister + 1	Mother + sister + 2
Toni#	♀	2003		Sister	Sister
Daisey	♀	2004		Mother	Mother + 3
Taylor^	♀	2004			Mother + sister
Mary	♀	2005			1
Long John	♂	2006			
Max&	♂	2006			

~ mother died in 2007, prior to data collection

* passed away prior to data collection 2010

^ sibling pair

& sibling pair

mother died in 2008

Discussion

The present study shows that groups of chimpanzees that do not systematically differ in their genetic backgrounds and live in similar ecological environments can execute social behaviour in group-specific ways. The group differences in GHC style preferences were robust and consistent over time, augmenting the argument that the GHC behaviour provides an example of chimpanzees' capacity to adopt, maintain and transmit a group-specific behaviour that is social in nature (McGrew & Tutin, 1978). The emergence of the GHC behaviour in group 3 supports our interpretation of the GHC behaviour being a behavioural phenomenon that has the propensity to emerge naturally in chimpanzee groups, and reinforces the need for detailed analyses such as these that go beyond the presence-absence distinction to evaluate whether the behaviour occurs in varying styles across groups. Observations that the GHC behaviour spreads to naive individuals and that the first partner of new hand-claspers is most often the mother is consistent with previous research (Bonnie & de Waal, 2006) and provides evidence for the primary line of behavioural transmission in chimpanzees being along maternal lines.

Based on a large dataset, our results show that neighbouring groups of chimpanzees can differ in their social grooming behaviour. The finding that only two groups regularly engaged in GHC behaviour while this behaviour was (nearly) absent in the other two groups validates the original study by McGrew and Tutin (McGrew & Tutin, 1978). Furthermore, the finding that the neighbouring groups of chimpanzees have different GHC style preferences validates the more detailed studies by Nakamura & Uehara (Nakamura & Uehara, 2004) and McGrew and colleagues (McGrew et al., 2001). The use of mixed models allows us to draw the conclusion that the group-specific style preferences were shared by most individuals within the respective groups, thus controlling for individual and dyadic preferences that could have influenced the results in the studies on the Mahale chimpanzees (McGrew et al., 2001; Nakamura & Uehara, 2004). In more detail, the *variation* of the GHC behaviour was robust in the sense that over the course of 2010-2012, the only two groups that engaged in the GHC behaviour showed stable differences in their style preferences. This result was found by comparing the chimpanzees' preferences at two different

points in time (one-year interval) using a large number of observations, and was corroborated by the observations of the year-round data collection procedure. Furthermore, the GHC behaviour has been observed for more than nine years in the Chimfunshi chimpanzees, indicating that the GHC behaviour is a stable part of the behavioural repertoire of the chimpanzees under study and surpassing the *durability* criterion (Perry et al., 2003). More importantly, the criterion of *expansion* has also been satisfied in this study as the results showed that the GHC behaviour spread to formerly naive subjects over time – in this case from one generation to the next (most often from mother to offspring). The dyadic nature of the GHC behaviour additionally indicates that GHC behaviour is not merely a behaviour that was individually discovered and maintained within one generation, but instead gets actively transmitted by means of social learning. The exact way in which the GHC behaviour gets transmitted, however, remains unclear. Opportunistic observations indicate that mothers mould their offspring's postures into the typical handclasp positions. Such directed postural guidance would preclude interpretation of handclasp transmission in terms of 'higher-level' mechanisms like emulation and imitation (e.g., Tomasello, 1999). However, where mothers have been observed to raise one arm of their offspring with one of their own arms in a way that resembles the GHC posture, these interactions have been observed in all four groups under study (KA Cronin & EJC van Leeuwen, pers.obs.). Thus, long-term observations are needed to elucidate how the group-specific preferences are transmitted and maintained over time. Notably, the group-preferences here reported were already existent in 2007 (EJC van Leeuwen, unpublished data) while five hand-clasping individuals of group 2 have been removed from their group over the course of 2007-2011. This further indicates that the GHC preferences are not limited to certain individuals but instead shared by most individuals of the group.

Recently, chimpanzees have been shown to exhibit group-specific preferences for nut-cracking techniques (Luncz et al., 2012). While traditions and cultures have been difficult to establish in animal societies because of confounding ecological and genetic factors (McGrew, 2004; Whiten & van Schaik, 2007; Laland & Galef, 2008), Luncz and colleagues report on group differences in nut-cracking behaviour within the same subspecies of chimpanzees, while at the

same time controlling for the most important environmental determinants (Luncz et al., 2012). The present study similarly reports on behavioural differences between neighbouring groups of chimpanzees, yet in the realm of social interactions instead of material behaviour. Not only does this make for the first robust evidence of social culture in chimpanzees, it also strengthens the claim for chimpanzee culture in general because ecological factors would seem more implausible to contribute to social compared to material differences. Whether the chimpanzee groups at Chimfunshi also differ along other social dimensions like play behaviour, proximity and aggression will be an exciting challenge for the future to explore (e.g., see Cronin et al., 2014).

Any ecological or genetic factor is unlikely to fully account for the findings of the present study for the following reasons: First, the four groups under study live in the same Miombo forest, and second, the groups do not systematically differ in their genetic composition. More importantly though, the group differences comprised *relative* preferences, meaning that all the GHC styles were in the behavioural repertoires of the two hand-clasping groups and thus that genetic influences can be ruled out even more compellingly. Finally, one important physical property of this social grooming behaviour (i.e., the arm-length differential) did not predict GHC style.

In this study, we have evaluated our findings against criteria that have been developed in order to decrease the likelihood that the behaviour under study is determined by non-social aspects like genetics and environment, and increase the likelihood that the behaviour under study is group-specific and socially transmitted (Perry et al., 2003; Whiten, 2003). Based on this assessment, we conclude that chimpanzees' social behaviour is not only motivated by innate predispositions and individual inclinations, but also partly cultural in nature.

Acknowledgements

This work was supported by the Psychology department of Gonzaga University and the Comparative Cognitive Anthropology research group of the Max Planck Institute for Psycholinguistics. The authors thank the Zambia Wildlife Authority, the Chimfunshi Wildlife Orphanage Trust founder and manager, Sheila Siddle and Innocent Mulenga,

respectively, the staff who provide care for the chimpanzees, and the Gonzaga University students for their assistance in data collection. A special thank you to Sam Freedgood, Marika Claire Groleau, Todd Gienger, Ben Sexton, Sarah Smith, Marloes van der Goot, Karoline Kneist, Maddalena Tacchetti and Vivian Vreeman. We thank W.C. McGrew, Susan Perry, Kristin Bonnie and one anonymous reviewer for valuable feedback on earlier drafts. This research complied with animal care regulations of PASA and internal guidelines of CWOT.

A group-specific arbitrary tradition in chimpanzees (*Pan troglodytes*)

Chapter 3

Based on:

Van Leeuwen, E. J. C., Cronin, K. A. & Haun, D. B. M. (2014). A group-specific arbitrary tradition in chimpanzees (*Pan troglodytes*). *Animal Cognition*

Abstract

Social learning in chimpanzees has been studied extensively and it is now widely accepted that chimpanzees have the capacity to learn from conspecifics through a multitude of mechanisms. Very few studies, however, have documented the existence of spontaneously emerged 'traditions' in chimpanzee communities. While the rigor of experimental studies is helpful to investigate social learning mechanisms, documentation of naturally occurring traditions is necessary to understand the relevance of social learning in the real lives of animals. In this study, we report on chimpanzees spontaneously copying a seemingly non-adaptive behaviour ("grass-in-ear behaviour"). The behaviour entailed chimpanzees selecting a stiff, straw-like blade of grass, inserting the grass into one of their own ears, adjusting the position, and then leaving it in their ear during subsequent activities. Using a daily focal follow procedure, over the course of one year, we observed 8 (out of 12) group members engaging in this peculiar behaviour. Importantly, in the 3 neighbouring groups of chimpanzees (n=82), this behaviour was only observed once, indicating that ecological factors were not determiners of the prevalence of this behaviour. These observations show that chimpanzees have a tendency to copy each other's behaviour, even when the adaptive value of the behaviour is presumably absent.

Introduction

Recapitulating the tenet of chapter 1: Social learning refers to learning about other agents or the inanimate world that is influenced by observation of, or interaction with, another individual or its products (Heyes 2012). A myriad studies have reported social learning in a variety of species (reviewed in e.g., Galef 2012). In nonhuman primates, many social learning studies have employed experimental designs using artificial target behaviours. While these experiments effectively explore learning capacities in the absence of confounding variables, the ecological validity of their results is inevitably restricted. To investigate how social learning is actually rather than plausibly employed in the lives of animals, documentation of naturally-occurring cases, like handclasping, is essential.

In addition to tracking the spread of behaviour within a single population, researchers have reasoned about the presence of social learning in nonhuman animals (henceforth “animals”) by reporting on intra-specific between-group differences that are unlikely to have emerged from non-social mechanisms (see (Wrangham et al. 1994). As explained in chapter 1, this “ethnographic approach” has been criticized for not being able to disentangle the contributions of genetic and ecological factors to the behavioural variation (Laland and Janik 2006). However, when multiple, isolated populations are present in the same ecological environment, this approach gains power.

In this study, we report on chimpanzees spontaneously copying a seemingly non-adaptive behaviour: Sticking grass in one’s own ear. Importantly, we present data on four groups of chimpanzees that live in the same forested environment and do not systematically differ by subspecies making the ethnographic approach powerful in this case (also see chapter 1 and 2).

Methods

Subjects

Subjects were 94 chimpanzees across four social groups at the Chimfunshi Wildlife Orphanage Trust, a sanctuary in the north-western part of Zambia (for details, see chapter 1 and 2). Except for Group 3 and 4, none of the groups can see each other. The chimpanzees stay outside overnight and only come indoors for supplementary mid-day feeding (11:30-13:30). All groups were

formed based on the order of arrival. Only non-infant chimpanzees were included in this study; infants were considered not old enough to copy or engage in the behaviour described in the following section.

The invention

“Grass-in-ear behaviour” (henceforth “GIEB”) was first documented in 2010 when the first author observed one female chimpanzee (Julie) repeatedly putting a stiff, straw-like blade of grass in one or both of her ears. She left the grass hanging out of her ear(s) during subsequent behaviour such as grooming, playing and resting (Figure 1); the behaviour served no discernible purpose. Moreover, no ear infections were diagnosed in any of the chimpanzees at Chimfunshi during a thorough health check in October 2013.



Figure 1. Julie (the inventor) displaying the grass-in-ear behaviour.

Data collection and analysis

During subsequent visits to the sanctuary we observed that GIEB was also shown by other chimpanzees in the same social group. In order to determine whether the GIEB was transmitted via social learning, we analysed one year of videos derived from a focal follow procedure that started in February 2011 and

yielded 740 hours of (video) observation through February 2012 (Group 1–4: 184, 201, 159, and 166 hours, respectively). Data were collected for one hour on each group daily, and consisted of ten-minute focal follows centered on a subject that was chosen through systematic sampling of the enclosure. Focal follows included a minimum of 2-meter visibility around the focal subject (for details see chapter 2 and Cronin et al., 2014). We operationalized GIEB as “putting grass in one’s own ear”. In addition to scoring all occurrences of GIEB (scored as present or absent for each individual in each focal follow), we scored whether GIEB occurred simultaneously by more than one individual. In order to test our hypothesis that the GIEB was sparked by social processes rather than by repeated individual inventions, we analysed the likelihood of the observed distribution of GIEB over all subjects across the four social groups given a randomly assigned distribution with a two-sided Fisher’s exact test with simulated *P*-value (Monte Carlo randomizations). Additionally, the frequency of GIEB co-occurrences was investigated to i) analyse whether social learning could have taken place (i.e., social learning requires proximity), and ii) to possibly shed light on the learning mechanism(s) involved. After the GIEB inventor passed away on May 22nd 2013, we analysed all available Group 4 data collected afterwards (up to July 14th 2013, yielding 25 hours of observation) in order to investigate whether the GIEB outlasted its inventor.

Results

GIEB was only observed in one of the four chimpanzee groups (Group 4), with the exception of one occurrence in one other group (Group 2). In total, 8 of 12 chimpanzees of Group 4 were observed to (repeatedly) engage in GIEB by February 2012 (Table 1: also see Figure 2 for the diffusion of GIEB through Group 4 over time and Figure 3 and 4 for GIEB examples).

Table 1. GIEB only diffused in one of the four neighbouring groups of chimpanzees at Chimfunshi: Given are the occurrences of GIEB of all individuals in Group 4 as observed in the focal follow videos over the course of February 2011 – February 2012.

	<i>Sex</i>	<i>Age</i>	<i>GIEB (frequency)</i>
Julie*	female	18	168
Kathy	female	13	36
Val	male	12	10
Jack	male	4	8
Miracle	female	11	7
Sinkie	male	18	2
Bobby	male	18	1
Nicky	male	21	1
Kambo	female	16	0
Bertha	female	12	0
Commander	male	12	0
Kit	male	7	0

*Inventor of the GIEB

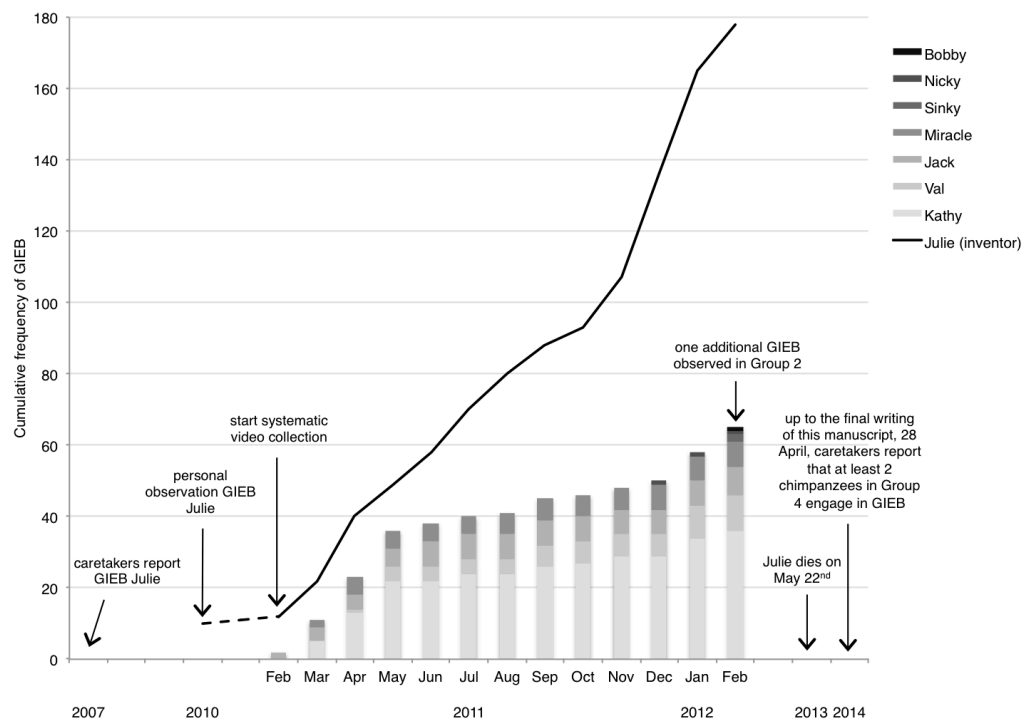


Figure 2. Cumulative record of GIEB in Group 4 at the Chimfunshi Wildlife Orphanage Trust for Julie the inventor (black line) and the imitators (stacked bars) separately. Julie was reported to engage in GIEB in 2007 by the chimpanzee caretakers, which was verified by informal observation of at least 10 GIEB bouts by the first author in 2010. No other chimpanzees were reported or observed to engage in GIEB at that time. After Julie's death in June 2013, 7 GIEB bouts (2 individuals) have been observed during systematic analysis of additional video material up to the 15th of July 2013 (see *Methods* and *Results*). By the time of the final writing of this manuscript, the 28th of April 2014, the same 2 chimpanzees as were observed in the videos between June 3rd and July 14th (Kathy and Val) still engage in GIEB.

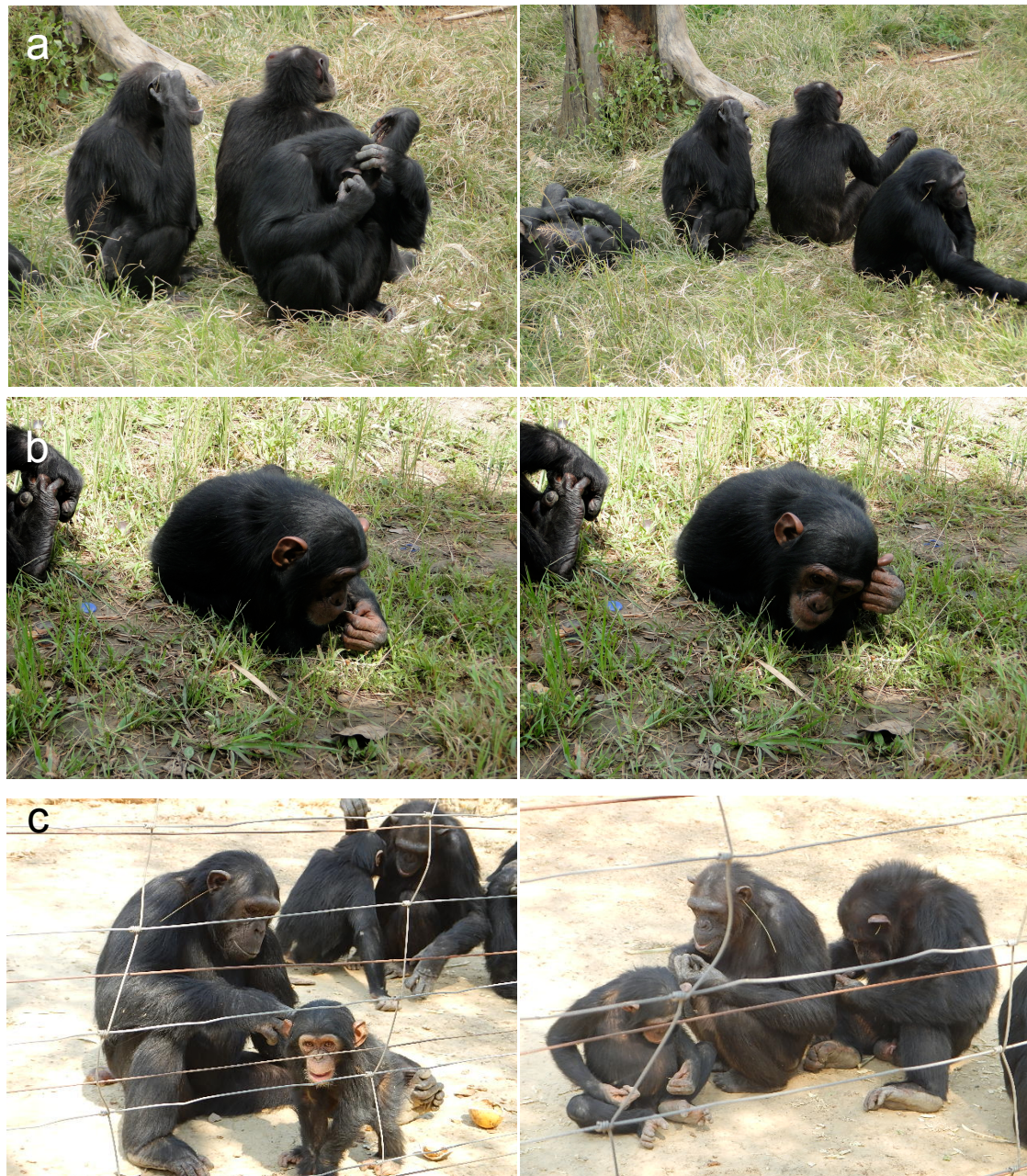


Figure 3. Grass-in-ear behaviour examples in the chimpanzees of Group 4 at the Chimfunshi Wildlife Orphanage Trust: (a) After Julie has stuck grass in her ear (individual on the left in the left photo), Kathy starts doing the same (left) and succeeds (right); (b) Jacky (Julie's son) lies in front of Julie, suckling on a straw of grass (left) after which he attempts to put it in his ear (right); (c) Kathy grooms Kenny while keeping a straw of grass hanging out of her right ear (individual on the left in the left photo); Julie sits behind Kathy on the right in the left photo holding a piece of grass in her right ear; Jacky is attempting to suckle from her breast); a little later, Val sits behind Julie and sticks a piece of grass in his ear (individual on the right in the right photo) after Julie had set the example (Jacky is fiddling with a piece of grass in front of Julie). *Photo courtesy: (a-b) Katherine Cronin; (c) Mylène Désilets.*

The distribution of GIEB subjects over the four social groups was unlikely to be random (Fisher's exact test: $P < 0.0005$). Apart from the GIEB of the inventor, in Group 4, almost all GIEB occurrences were observed simultaneously with the GIEB of at least one other individual, the GIEB inventor ($61/65 = 93.8\%$ of the cases). Finally, two individuals (Kathy and Val) were observed to engage in GIEB after the inventor had died (2 and 5 times, respectively), none of those times simultaneously. Up to the final writing of this communication (28th of April, 2014), both Kathy and Val have been engaging in GIEB (pers. comm., Innocent Chitalu Mulenga, manager at Chimfunshi; see Figure 2).

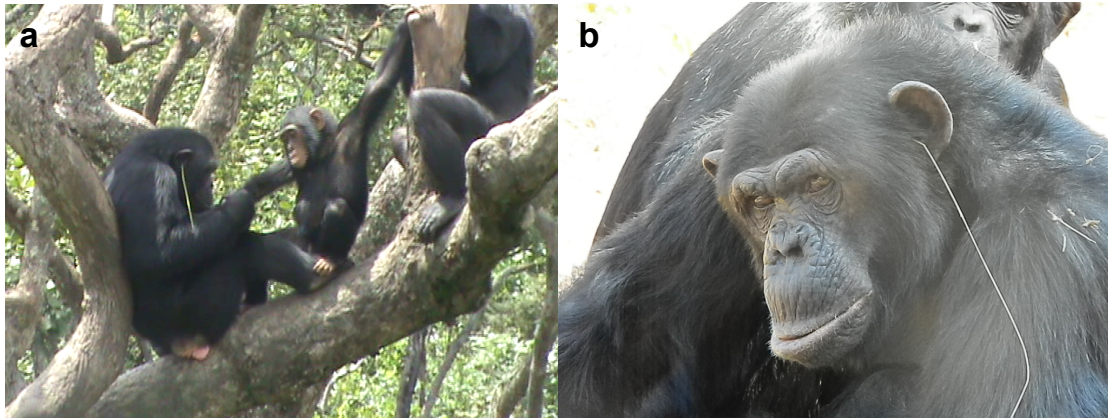


Figure 4. Further grass-in-ear behaviour examples in Group 4: (a) Kathy (left) grooms Jack (middle) up in a tree, together with Julie (right). Both Kathy and Julie engage in the GIEB (only Kathy's GIEB is visible here); (b) Val is being groomed by Kathy while he engages in the GIEB.

Discussion

This study reports the existence of a non-adaptive behavioural tradition in untrained chimpanzees. The behaviour consisted of putting a straw of grass in one's own ear and while it occurred frequently and by the majority of individuals in one group, it was only observed once across the three other groups of chimpanzees. Since the chimpanzee groups at Chimfunshi live in one continuous woodland and do not systematically differ by subspecies, it is difficult to imagine that ecological and/or genetic factors caused the disproportionate concentration of GIEB individuals in one group. Further taking into account that most GIEB events occurred in proximity to another individual engaging in the GIEB, it seems parsimonious to interpret the observations in terms of a socially learned behavioural pattern.

In a recent study investigating the strength of associations within and between groups (Cronin et al. 2014), where association is defined as frequency with which individuals are observed in proximity to one another, Julie's highest association score was with her son, Jack, who was the first chimpanzee observed to acquire the GIEB. She also associated more with Kathy, the second chimpanzee observed to acquire the behaviour, than she did on average with other chimpanzees in the group. The next two imitators, Miracle and Val respectively, had average association scores with Julie, but approached Julie more frequently than the average approach tendency in the group. These data indicate a relationship between proximity and social learning as has been seen in other research (e.g., Bonnie & de Waal, 2006), but given the nature of the behaviour and the observational schedule, we cannot establish a definite link.

Natural observations like the ones described in the present report are important for they show that social learning occurs spontaneously amongst chimpanzees (as opposed to experimentally imposed / rewarded; also see Whiten et al. 1999). As such, the GIEB may be reminiscent of chimpanzees' tool use acquisition (e.g., Luncz et al. 2012) or grooming handclasp behaviour (e.g., van Leeuwen et al. 2012). However, the GIEB observations may be additionally informative because the chimpanzees adopted a behaviour that is not an obviously functional manipulation of the physical world (as in the tool-use context) or the social environment (as in the grooming handclasp context). Due

to its spontaneous and arbitrary nature, the GIEB may be most comparable to the observation that able-bodied chimpanzees copied a motor procedure from a chimpanzee who had been handicapped by a snare trap and was therefore forced to scratch his back in an unorthodox way (Hobaiter and Byrne 2010). Those authors concluded that because the able-bodied chimpanzees could scratch themselves in chimpanzee-typical ways, they copied an “unnecessary behavioural trait” (Hobaiter and Byrne 2010). In conjunction, these observations on chimpanzees’ propensities to imitate unnecessary actions are reminiscent of human’s arbitrary manners, like dinner etiquette or dress-codes. The unique property of the grass-in-ear tradition might be that the respective behaviour is not even remotely related to any of chimpanzees’ functional actions. Whereas the GHC tradition could be understood as an arbitrary modification (palm or wrist) of one of chimpanzees’ most typical behaviours (grooming), the grass-in-ear fad has come into existence out of an entirely novel invention. The fact that chimpanzees copied this novel, functionless behaviour uniquely shows that chimpanzees might have a rudimentary reward-system for copying behaviour regardless of immediate adaptive value (i.e., a pivotal characteristic of humans, leading to exponential cultural expressions). In turn, this conjecture could be put to the test in future research (cf. Bonnie & de Waal, 2007).

As for the transmission, the GIEB fad might be best explained by lower-level mechanisms. Since GIEB almost exclusively occurred simultaneously, response facilitation seems a likely mechanistic explanation. Even though this mechanism commonly refers to triggering familiar behaviour (Rendell et al. 2011), the novel sequence of putting grass in one’s own ear may fit the scope of this mechanism (Byrne and Russon 1998). On the other hand, imitation could have been at play. It could be argued that the novelty of putting grass in one’s own ear was sufficient to classify the GIEB copying as imitation (e.g., Tomasello, 1999, Whiten & Ham, 1992). The simultaneous occurrence of GIEB could be explained by the fact that individuals needed time and an immediately accessible GIEB example to mimic their actions off of. Note that this mimicking part is not trivial: instead of manipulating a shared object in the environment, the chimpanzees had to transform their visible input (seeing another chimpanzee

putting grass in her ear) into an action directed to themselves. Based on these considerations, imitation might be the most likely transmission mechanism involved in the GIEB fad.

The observation that GIEB was also observed in isolation may indicate that while response facilitation or imitation had broadened the repertoires of the copycats, only some experienced the behaviour as somehow rewarding and continued engaging in it on their own (Galef 1995). Furthermore, the fact that no ear infections were found in any of the chimpanzees in 2013 indicates that at least Kathy and Val do not merely put grass in their ears in response to a physical problem (they both still engaged in GIEB in 2014, pers. obs.). Finally, in conjunction with its arbitrary nature, the perpetuation of socially learned behaviour in the absence of the original inventor, despite its low frequency, links the GIEB observations to human cultural phenomena (Boesch 2013).

Regardless of the precise mechanism underlying the behavioural diffusion, our observations show that chimpanzees spontaneously copy arbitrary behaviour from their group members. In line with Hobaiter & Byrne (2010), we interpret our data as reflecting chimpanzees' proclivity to actively investigate and learn from group members' behaviours (and their consequences) in order to obtain biologically relevant information. The fact that these behaviours can be arbitrary and outlast the originator speaks to the cultural potential of chimpanzees.

Acknowledgements

The authors are grateful to the Zambia Wildlife Authority and the Chimfunshi Wildlife Orphanage Trust for hosting this project. Many thanks to Innocent Chitalu Mulenga (CWOT manager), the Chimfunshi staff (Patrick Chambatu, Thomson Mbilishi, Albert Mulembo, Goodson Muletele, Felix Chinyama, Patrick Mwika, Mumba Kawele, Misheck Kasongo, John Kayuya and Joseph Kasongo), Ian Ferreira and the video coding team in Nijmegen including Vivian Vreeman, Marjolein van Ginneken, Karoline Kneist, Rebecca Koomen and Maddalena Tacchetti.

Conformity in nonhuman primates: Fad or Fact?

Chapter 4

Based on:

Van Leeuwen, E. J. C. & Haun, D. B. M. (2013). Conformity in nonhuman primates: Fad or Fact? *Evolution & Human Behavior*, (34), 1-7.

Abstract

Majority influences have long been a subject of great interest for social psychologists, and now more recently, for researchers investigating social influences in nonhuman primates. Although this empirical endeavour has culminated in the conclusion that some ape and monkey species show 'conformist' tendencies, the current approach seems to suffer from two fundamental limitations: i) Majority influences have not been operationalized in accord with any of the existing definitions, thereby compromising the validity of cross-species comparisons, and ii) The results have not been systematically scrutinized in light of alternative explanations. In this review, we aim to address these limitations theoretically. First, we will demonstrate how the experimental designs used in nonhuman primate studies can not test for conformity unambiguously and address alternative explanations and potential confounds for these published results in form of primacy effects, frequency exposure and perception ambiguity. Second, we will show how majority influences have been defined differently across disciplines and, therefore, propose a set of definitions in order to streamline research on majority influences where *conformist transmission* and *conformity* will be put forth as operationalizations of the overarching denominator *majority influences*. Finally, we conclude with suggestions to foster the study of majority influences by clarifying the empirical scope of each proposed definition, exploring compatible research-designs and highlighting how majority influences are contingent on situational trade-offs.

1. Introduction

While humans are arguably the most creative and innovative of species, they sometimes seem to give precedence to majorities beyond reason. In a seminal set of studies, Solomon Asch showed that a substantial proportion of adult subjects would forgo their personal opinion when confronted with an erroneous but unanimous group of peers (Asch, 1956). These findings have been replicated across cultures (Bond & Smith, 1996) and in children as young as four years of age (Walker & Andrade, 1996; Haun & Tomasello, 2011). Possible reasons for this seemingly irrational behaviour are the benefits of group-life, where avoiding social conflict through reducing behavioural dissimilarity plays an important role (Over & Carpenter, 2011), and the benefits of relying on the wisdom of the crowd, where discounting personal preferences in favour of the majority strategy on average reaps safer, more reliable and more productive information (Boyd & Richerson, 1985; Henrich & Boyd, 1998; King & Cowlishaw, 2007). Where giving precedence to majority strategies can reap both social and informational benefits, it has also been advocated as one of the driving forces behind cultural diversification. In theory, adopting the behaviour displayed by the majority of individuals will produce within-group homogeneity, whereas the between-group heterogeneity will be accentuated (given initial between-group differences). As such, the tendency to ‘conform’ to what most others are doing has been associated with the evolution of human cultures (Boyd & Richerson, 1985; Henrich & Boyd, 1998; Efferson et al., 2008; Claidière & Whiten, 2012).

In recent years, researchers have started to address majority influences in nonhuman animals in general (Day et al., 2001; Galef & Whiskin, 2008; Pike & Laland, 2010), and nonhuman primates (hereafter called ‘primates’) in particular (Whiten et al., 2005; Bonnie et al., 2007; Dindo et al., 2008; Dindo et al., 2009; Perry, 2009; Pesendorfer et al., 2009; Hopper et al., 2011). The investigation of several related primate species enables us to investigate the phylogenetic distribution and history of majority influences, as well as the evolutionary processes that may have driven their evolution, thus shedding light on the evolutionary roots of this perplexing human behaviour (MacLean et al., 2012). The endeavour to study majority influences commensurably and compare the extent to which humans and primates are affected by majorities, however, seems

in need of clarification (Galef & Whiskin, 2008; Pesendorfer et al., 2009). For instance, whereas social psychologists have used the term ‘conformity’ to describe the tendency to forgo individual information in favour of the majority opinion (Sherif, 1936; Asch, 1956; Bond & Smith, 1996), cultural evolutionary models have operationalized ‘conformity’ as the disproportionate tendency to copy the behaviour that is most frequent in a given population (Boyd & Richerson, 1985; Henrich & Boyd, 1998). In this review, we evaluate the validity of the operationalizations used in the recent primate studies and aim to calibrate the study of majority influences by providing a conceptual and methodological framework.

2. Is primates’ behaviour affected by majorities?

While not originally setting out to investigate majority influences, recent primate studies (Whiten et al., 2005; Bonnie et al., 2007; Dindo et al., 2008; Dindo et al., 2009; Hopper et al., 2011) have culminated in the conclusion that primates show ‘conformist’ behaviour (Claidière & Whiten, 2012). The shared ground on which these studies build their conclusions is the observation that subjects tend to revert back to their socially learned solution of a ‘2-action problem’ after discovering an equally effective alternative individually (the design used in these studies will hereafter be referred to as ‘reversion design’). Since their first solution was also acquired by most group members, the subjects seemingly revert back from a new innovation to the majority strategy. The critical problem, however, is that by seeding only one method in an isolated group of naïve primates, the subjects lack the crucial choice between the majority- and minority strategy needed to investigate majority influences. One could argue that the ‘corruptions’ from the first learned behaviour may function as minority demonstrations for opportunistic bystanders; yet, these demonstrations will have to compete with an established and reliably reinforced behavioural contingency, deeming any conclusions on majority influences confounded with maintaining familiar and reliable information.

In the following sections, we will present an alternative explanation for the observation that primates revert back to the majority behaviour (§2.1) and show how the interpretation of ‘conformist’ behaviour is confounded by

frequency exposure (§2.2), perception ambiguity (§2.3) and inherent study-design limitations (§2.4). Subsequently, we will show that the majority-influence definitions across research disciplines are currently inconsistent and propose a set of definitions in order to streamline majority-influence research – *conformist transmission* and *conformity* – where we will stay close to the definitions as they have emerged within the respective research traditions and outline the empirical scope of each definition by means of a thought experiment (§3.1). Finally, we will address study designs that would test for the different kinds of majority-influences accordingly (§3.2) and explore some further considerations to advance the study of majority influences more generally (§3.3). In conjunction, this discussion should allow for a more valid interpretation of primates' behaviour in the employed reversion-designs and offer conceptual and methodological tools for studying majority influences across species more commensurably.

2.1 Primacy effects

One of the most crucial difficulties in the current study of majority influences in primates is the possible confounding influence of primacy effects. When primates first become familiar with the method that later becomes the majority strategy, and do not discover the equally effective alternative strategy until the first method has become fairly well ingrained, it seems impossible to reliably attribute their 're-convergence with the majority strategy' (Whiten & van Schaik, 2007) to a majority influence. First of all, in certain studies, the discovery of the alternative strategy could be accidental as the two available strategies to solve the 2-action problem could arguably be conceived of as structurally similar (Dindo et al., 2008; Dindo et al., 2009). This means that the subjects might not actually *learn* the alternative strategy, which in turn means that instead of 'reverting back', the subjects *continue* using their first learned behaviour. Second, even if the subjects *learn* to use the alternative strategy, the first learned strategy will be more ingrained through repetitive and reliable reinforcement, which deems any comparison of social arguments for using one strategy over the other unfair. Moreover, in the respective studies, the subjects that learned to use both strategies most likely did so in a qualitatively different way: the first strategy

socially and the alternative strategy individually (e.g. in Whiten et al., 2005; Bonnie et al., 2007; Dindo et al., 2009). Since research has shown that animals can weigh socially acquired information differently than individually acquired information (for reviews, see Kendal et al., 2005; Kendal et al., 2009), this aspect too needs to be balanced between strategies in order to be able to attribute the behavioural choices of subjects in terms of majority influences. Finally, at least in chimpanzees (Marshall-Pescini & Whiten, 2008; Hrubesch et al., 2009) and marmosets (Pesendorfer et al., 2009), preferring the strategy that first entered the behavioural repertoire over subsequently discovered strategies might be more parsimoniously explained by a high level of conservatism. While conservatism has been rejected as explanation for the observed within-group homogeneity of behavioural strategies in favour of conformity in chimpanzees (Hopper et al., 2011), we believe that the extent to which conservatism can exert effect on behaviour should be revisited. Based on the premise that the frequency and intensity of previous experiences impact individuals' future decisions, in our view, *conservatism* entails any mechanism that after mastering a strategy decreases the likelihood of performing a novel behaviour in the same stimulus-response domain, where the learning curve for the acquisition of the first strategy should be the benchmark to judge this likelihood. Importantly, this definition leaves open the possibility of prior knowledge impeding the adoption of a new behavioural strategy *even after this strategy has been explored*, deeming the rejection of conservatism in favour of 'conformity' in the primate studies premature (Hopper et al., 2011) (The relation between the impact of previous knowledge on future behaviour and majority influences will be discussed in section 3.3). An early social learning study in chimpanzees seems to illustrate this matter succinctly, while at the same time indicating that conclusions on majority influences require proper caution. In this study, chimpanzees preferentially used their first learned action-pattern that was demonstrated to them by a human experimenter, even after discovering that other sequences worked equally well (Whiten, 1998; also see Whiten & van Schaik, 2007). In our view, this study shows that chimpanzees will also retain their first learned behaviour in the absence of a majority (of conspecifics) and that their conservatism is not necessitated by an inability to perform alternative actions

(just like in the reversion designs, see Whiten et al., 2005; Bonnie et al., 2007; Dindo et al., 2008; Dindo et al., 2009; Hopper et al., 2011).

2.2 Frequency exposure

Another important matter for the study of majority influences is the nature of the strategy distribution within the population. In principle, the overall *frequency* by which strategies are being used is independent from the number of *individuals* using the same strategy. Since both variables can serve as information source for others, it remains an empirical challenge to infer which social learning bias subjects use in the process of adopting cultural variants. Whereas Perry (2009) used the absolute frequency exposure as a measure to advocate 'conformism' in capuchin monkeys, a recent study in chimpanzees separates the effects of *frequency* and *individuals*, finding that the majority of individuals, but not the equivalent frequency, predicts naïve subjects' tendency to adopt the demonstrated cultural variant (Haun et al., 2012). Hence, for conceptual and empirical reasons, we propose to separate majority influences (in terms of individuals) from effects that might be exerted through absolute frequency of repeated behaviours (cf. Claidière & Whiten, 2012).

2.3 Perception ambiguity

As a prerequisite for any majority influence, subjects need information on the behavioural distribution within their group. Since instantly obtaining knowledge of the full distribution seems unlikely outside the experimental setting, subjects will either sample subsets of the group instantly or engage in sequential sampling. Importantly, both these sampling methods are prone to distortions from the overall (objective) strategy distribution, necessitating a more subjective approach to the study of majority influences. In most primate studies, however, the objective knowledge of the strategy distribution seems to be falsely equated with the subjects' perception records. One recent study in chimpanzees does report the average number of their observations of a target behaviour per study group (Hopper et al., 2011). However, while this study sets the right example, it remains unclear *which* strategies the subjects had observed and whether their observations tallied up to the perception of the same strategy

distribution as the authors have assumed in their conclusions. In other words, while some subjects might have been influenced by a *perceived* majority, others might have copied a minority yielding the same end-result.

2.4 Further limitations of the ‘reversion’ design

The observation that individuals are inclined to revert back to their first learned behaviour after discovering an equally effective alternative does not justify the claim that those individuals are conformists. Besides the above-mentioned confounds, the reversion design does not seem to test for majority influences in any conventional way: First, the individuals that are designated ‘conformists’ in this paradigm are the only ones that *diverge* from the ‘group norm’ at some point in time, and second, rather than having to *change* their behaviour in order to match the majority, the designated ‘conformists’ need to *maintain* their most familiar strategy (Whiten et al., 2005; Bonnie et al., 2007; Dindo et al., 2008; Dindo et al., 2009; Perry, 2009; Pesendorfer et al., 2009; Hopper et al., 2011). Furthermore, and perhaps even more essential to the study of majority influences, in designs where only one strategy gets demonstrated (like in the reversion designs), it is impossible to infer that the majority per se was responsible for any modifications in behaviour. First, a majority by definition needs a minority (and thus an alternative strategy demonstration), and second, distinguishing between adopting the strategy that gets demonstrated *socially* and the bias toward copying the social information that gets demonstrated by the *majority* of individuals requires comparisons between the extent to which different numbers of demonstrators affect the observers’ behavioural decisions (see section 3.2). These considerations may be pivotal in demarcating majority influences from other social influences, thereby aiding both the study of species-typical social learning behaviour and the cross-species comparison of conformist tendencies. Finally, in the reversion scenario, any claim of ‘conformity’ as it has been advanced in the cultural evolution literature (Boyd & Richerson, 1985; Henrich & Boyd, 1998; Mesoudi, 2009) would be problematic, since with only one strategy seeded, there is no way to test whether the tendency to copy the majority is *disproportionate* to the relative size of the majority. As will become clear in the next section on the scope of the different

majority-influence operationalizations, without such a stringent criterion, it is impossible to conclude that individuals *preferentially* adopt the majority strategy (see Mesoudi, 2009).

In order to elucidate what we can possibly learn from primates' behaviour in the reversion designs and to streamline the cross-species comparison of conformist behaviour in general, we will now turn to the operational definitions of majority influences. Subsequently, we will propose designs that would test for the different majority influences more validly.

3. Comparing apples and oranges; a proposal for calibration

As several scholars have pointed out, the study of 'conformity' is currently convoluted (Efferson et al., 2008; Galef & Whiskin, 2008; Mesoudi, 2009; Pesendorfer et al., 2009; Claidière & Whiten, 2012). For example, while originally used to describe the adjustment of one's conviction to a majority position (Asch, 1956), conformity was more recently invoked to describe the tendency to revert back to the first learned behaviour after discovering an equally effective alternative (Whiten et al., 2005). Misguided by such operational mismatches, researchers have investigated different processes under the same banner of 'conformity', not only leading to preliminary conclusions on species' behavioural repertoires, but also clouding the perspective on the evolutionary roots of conformist behaviour (Claidière & Whiten, 2012). Hence, in order to assess animals' behavioural tendencies more validly, we propose a set of definitions with the aim to distinguish majority influences from other learning effects and dissect the different ways in which majorities can affect the behaviour of observers.

3.1 Majority influence definitions

We propose to use the term 'majority influence' to refer to all instances where the very presence of a majority affects the behaviour of observers. Importantly, here, we define these effects in terms of behavioural end-results, not mechanisms. We argue that the confusion in majority-influence terminology at least in part stems from the confounding of mechanisms and end-results.

Where the mechanism under study is the bias to *copy-the-majority* (Laland, 2004), the means to investigate this bias have typically been operationalized as different magnitudes on the probability continuum of adopting the majority strategy. For instance, majority influence has been defined in terms of ‘an increased likelihood to adopt the majority strategy compared to the expectation in absence of any inherent or social biases for one cultural variant over the other’ (see ‘linear imitation’ in McElreath et al., 2005; ‘weak- and linear-conformity’ in Claidière & Whiten, 2012; and ‘majority-biased transmission’ in Haun et al., 2012). One possible mechanism that would lead up to this end-result is where individuals copy one of multiple demonstrators at random: in the presence of a majority, they will be more likely to copy the cultural variant that the majority of individuals employ (see Mesoudi, 2009). Similarly, when the relative size of the majority is significantly bigger than the probability of adopting a cultural variant in the absence of any biases (e.g., majority proportion = 0.8, unbiased adoption probability = 0.5), the presence of a majority may even increase the likelihood to adopt the majority strategy of individuals that learn by accommodating and persevering in the first observed behaviour (see section 2.1 on primacy effects). Albeit seemingly trivial, without a majority, these individuals would have been less likely to adopt the respective majority strategy, and thus acquire the cultural variant that has been postulated to be relatively adaptive (Boyd & Richerson, 1985; Henrich & Boyd, 1998; King & Cowlshaw, 2007).

A more stringent effect of the presence of a majority has been operationalized by adhering to the criterion of a *disproportionate* likelihood to adopt the majority strategy. In this case, the probability for an individual to end up with the majority strategy is not only higher than expected in absence of any inherent or social biases for one cultural variant over the other, but also higher than the relative size of the majority in the population (this scenario is called ‘conformist transmission’, see below). In principle, these differently operationalized majority influences do not presuppose any specific mechanism(s): since the *majority* by definition comprises most individuals in a given group, and thus likely affords a multitude of (social) learning strategies to be triggered (Laland, 2004; Kendal et al., 2005), ending up with the majority

strategy can be caused by different (interacting) mechanisms. However, even though the increased likelihood to adopt the majority strategy is interesting in its own right (see Haun et al., 2012), the identification of the underlying mechanism(s) is important for reasons of pinpointing the source of behavioural modification and thus individuals' capacities and/or inclinations. Moreover, knowledge of the underlying mechanism would be necessary for any valid cross-species comparison and thus for investigating the evolutionary roots of majority influences (MacLean et al., 2012). Therefore, in the remainder of this review, we outline the majority influence operationalizations that have typically been used to assess the existence of a copy-the-majority heuristic, investigate the extent to which the behavioural end-results delineated by these operationalizations relate to the potential underlying mechanisms and explore ways to further augment the study of the copy-the-majority heuristic.

Conformist transmission refers to the disproportionate tendency of naïve individuals to copy the behaviour of the majority (Boyd & Richerson, 1985; Henrich & Boyd, 1998; Efferson et al., 2008; Mesoudi, 2009). Thus, in the case of conformist transmission, the probability for an individual to end up with a certain cultural variant is not only higher than expected in absence of any inherent or social biases for one variant over the other, but also higher than the relative size of the majority in the population, thereby excluding the possibility that individuals are 'merely' copying others at random (Mesoudi, 2009). For instance, if we consider a population where a majority of individuals perform behaviour A ($N=17$) and a minority behaviour B ($N=3$), we would only refer to conformist transmission when the probability for a naïve immigrant to adopt behaviour A would be significantly higher than $p=0.85$ ($17/20$) (for an empirical example in humans, see Morgan et al., 2011). Note, however, that this definition refers to a behavioural end-result, not to a mechanism. Where the copy-the-majority strategy would yield this behavioural outcome, other learning heuristics that are consistently afforded by the majority may equally well explain the observed effect. For instance, under the assumption that the majority strategy is relatively adaptive because it is an aggregate of individual learning outcomes, it is not untenable to postulate that the majority is consistently comprised of the most proficient individual learners. Hence, the strategy to copy the most skilful

individual could potentially superimpose the strategy to copy the majority. Thus, even though random copying can be excluded by adhering to the criterion of *disproportionate* copying, the actual mechanism by which naïve individuals end up with the majority strategy remains unclear. In our view, this consideration should be pivotal to the study of majority influences: Do individuals copy the majority strategy *because* it is the majority strategy or do they copy the majority for some other reason that is consistently afforded by the majority? We will elaborate on this quandary in section 3.2.

Conformity refers to the tendency to forgo personal information by adopting the cultural variant that is used by the majority (Asch, 1956; Whiten & van Schaik, 2007; Haun & Tomasello, 2011). This term has emerged in the realm of human social psychology and has been used to describe the process in which human adults adjust their personal conviction to the unanimously expressed yet conspicuously erroneous conviction of the majority (Asch, 1956). While conformity entails the same adoption of the majority strategy as in the scenarios described above, it pertains to a different behavioural process in the sense that a familiar cultural variant needs to be abandoned in favour of another cultural variant. The criterion of adopting the majority strategy with a probability higher than chance or the relative size of the majority does therefore not apply to conformity: under the premise of equal cultural variant affordance (equally effective, intuitively appealing, etc.) and controlling for individual differences in exploration tendencies, every *change* in behaviour can be attributed to the social context. For instance, when an individual has acquired solution A to a 2-action problem, one could investigate its tendency to conform by calculating the difference in probability to forgo solution A for solution B between the situation in which the individual has no knowledge of the other group members' solutions versus the situation in which the individual has been exposed to a majority of group members using solution B. While the primate studies using the reversion designs base their conclusions on those individuals that acquire both of the available strategies, they fail to show how the subjects would respond in a non-social environment (see Whiten et al., 2005; Bonnie et al., 2007; Dindo et al., 2008; Dindo et al., 2009; Hopper et al., 2011). Especially in studies where the two available solutions might be perceived as structurally similar (Dindo et al., 2008;

Dindo et al., 2009), this non-social control condition would be additionally necessary to be able to attribute the observed behavioural patterns to majority influences (also see Morgan & Laland, 2012).

Similar to the case of conformist transmission, however, the mechanism behind the behavioural change should be additionally scrutinized in light of the plethora of potential (social) learning biases (see Laland, 2004; Kendal et al., 2005; Rendell et al., 2011; Claidière & Whiten, 2012): Where majorities could be influential in their own right, the individual members comprising the majority could equally likely exert effect on observers' decision-making processes. By adhering to the criterion of disproportionately copying the majority, only 'random copying' can be excluded from the possible underlying mechanisms (for 'conformity', see Pike & Laland, 2010; for 'conformist transmission', see Morgan et al., 2011). In the next section, we will propose ways to further reduce the ambiguity of mechanisms revolving around majority influences and investigate the copy-the-majority bias more precisely.

3.2 Study design proposals

In this section, we will present study designs that would test for majority influences more validly, following the proposed set of operational definitions. Subsequently, in the next section, we will explore some further considerations that may help to improve the study of majority influences across species.

First, in order to study conformist transmission in primates more validly, we propose to adjust the designs in accord with some recent animal studies (sticklebacks: Webster & Hart, 2006; Pike & Laland, 2010; great apes: Haun et al., 2012). In these studies, focal individuals are presented with equivalent foraging patches, one demonstrated by the majority and one by a minority, and subsequently tested for their foraging preferences. Crucially, the choice-availability in this design allows for a more direct investigation of majority influences than the reversion designs, in which only one of the two possible strategies is seeded and hence demonstrated to the focal individuals. As long as focal individuals do not have a choice between a majority and minority strategy, and the demonstration and subsequent acquisition of available alternatives is

not fairly balanced in time and thus in perception records, results will remain hard to interpret in terms of majority influences.

Similarly, in order to study conformity validly, and hence facilitate the cross-species comparison, the primate studies could improve by mimicking the human designs more closely. Instead of letting the conformity choice coincide with the strategy that the focal individuals learn first (see Whiten et al., 2005; Bonnie et al., 2007; Dindo et al., 2008; Dindo et al., 2009; Perry, 2009; Pesendorfer et al., 2009; Hopper et al., 2011), the improved designs should investigate whether the focal primates would forgo their initial knowledge and/or preference in order to match the majority behaviour (see Asch, 1956; Bond & Smith, 1996). This way of operationalizing 'conformity' has also been integrated in the stickleback studies, where knowledgeable subjects were presented with majority vs. minority demonstrations, yielding strong indications that at least nine-spined sticklebacks show tendencies reminiscent of conformity as found in human subjects (see Pike & Laland, 2010; strictly speaking, the evidence for preferentially copying the majority is stronger in the stickleback study than in the human studies since the former presents evidence of subjects adopting the majority strategy *disproportionately*, while the latter are typically conducted using an unanimous 'majority', deeming it impossible to disentangle whether the focal individuals copy the majority or a (random) individual of the majority; see (Asch, 1956; Bond & Smith, 1996). For a recent study in human subjects showing more valid evidence of preferentially copying the majority, see Morgan et al., 2011). Note, however, that up till now, *personal knowledge* has not been dissected in terms of reinforcement histories or preferences. The importance of this dissection for understanding conformity behaviour will be addressed in section 3.3 (also see Chapter 6).

Finally, in order to be able to draw valid conclusions on the actual *preference* to copy the majority, one needs to take into account that a majority bias would almost inevitably coincide with other social learning biases that are predicted to be beneficial for social animals, like copy kin, prestigious individuals, or the most skilful individual (Laland, 2004). Therefore, in order to make sure that the focal individuals copy the majority per se and not the individuals in it (similar reasoning for a possible minority bias), the designs

should incorporate repeated measures of differently composed subgroups, where all the meaningful characteristics and relations of the involved individuals (like age, gender, bonds of affiliation, etc.) should be counterbalanced over trials. (Since characteristics like age, gender and demeanour could similarly exert effects through imagery, to a certain degree, the same reasoning would hold for video demonstrations). This consideration additionally exposes the empirical question as to what extent the relative size of the majority impacts the focal individual's behaviour; ranging from unanimous 'majorities' (Asch, 1956) to subgroups comprising the highest number of individuals without being the majority (i.e. 'pluralities', see Hastie & Kameda, 2005), majorities can differently affect decision-making processes in subtle yet crucial ways (see studies in humans: Coultas, 2004; Morgan et al., 2011; and sticklebacks: Pike & Laland, 2010).

3.3 Additional considerations for the study of majority influences

Another important aspect to consider in studying majority influences - one that is generally overlooked - is the character of the situation under study. For instance, in situations where individuals need to compete over *known* food resources, one might not expect majority influences at all, or if anything, the opposite effect: individuals would optimize their gains by avoiding foraging with the majority (the opposite might be true for exploring *new* foraging patches, see e.g. Day et al., 2001). Alternatively, in situations in which individuals need to coordinate their behaviour in order to gain benefits or avoid costs, one might expect majority influences to be highly present, or at least likely (see Eriksson et al., 2007). By taking into account the (nature of the) situational pressures that individuals are under, one could more reliably assess the relative importance for individuals to copy the majority. For instance, the incentive to follow the majority might be more pronounced for animals under high predation risk (e.g. nine-spined sticklebacks; see Pike & Laland, 2010) than for animals living in a relatively predictable environment, having acquired a perfectly safe and reliable strategy on their own (see Whiten et al., 2005; Bonnie et al., 2007; Dindo et al., 2008; Dindo et al., 2009; Pesendorfer et al., 2009; Hopper et al., 2011).

Similarly, the nature of the focal behaviour might differentially impact the extent to which majorities affect observers' behaviour. Where behaviours like foraging or prey avoidance can yield substantial fitness benefits if executed adequately, and thus costs if executed inadequately, behaviours like playing or grooming might be less strictly regimented by the anticipation of survival. In the former case, one could expect a majority bias to be highly rewarding in light of the fact that the majority strategies are aggregate responses of individuals sampling the environment with their unique tool-kits (physical and psychological instruments), thus amounting up to relatively adequate strategies (Boyd & Richerson, 1985; Henrich & Boyd, 1998). On the other hand, even with behaviours that pertain less directly to fitness benefits, like in the latter case, one could expect individuals to preferentially copy the majority of individuals: under the assumption that a social life offers benefits, the threat of ostracism can be a strong incentive for group members to imitate the behaviour of the subgroup with the most power, i.e. the majority (Over & Carpenter, 2011). Therefore, in any study investigating majority influences, it would be fruitful to elaborate on both the instrumental and social trade-offs that might pertain to the focal behaviour of the species under study. For instance, in a compatible token-design study, one should contemplate the relative incentive for chimpanzees to switch from using their first learned token-contingency to using the majority's token-contingency in terms of strategy efficiency and social acceptance and/or punishment. Perhaps, in this particular situation, the equation of incentives (instrumental and social) would yield the prediction that sticking to the first learned strategy would be the most adaptive strategy (e.g. both strategies work equally well, no uncertainty/risk pertaining to the outcome of using either strategy, relatively little opportunity for social control; see (Morgan et al., 2011) for an example of identifying the circumstances under which humans are most likely to copy the social information provided by the majority). Not merely an option, this consideration could prevent researchers from investigating majority influences under circumstances that do not predict forgoing personal information or adopting the majority strategy for behavioural optimization. Moreover, the framework in which behaviours and situations are scrutinized in

light of instrumental and social trade-offs would prove fruitful in identifying species-typical inclinations and thus in the realm of cross-species comparisons.

Finally, one of the critical features in predicting and determining the extent of conformity might be the psychological distance between the subject's familiar behaviour and the majority strategy. In line with factors related to environmental oscillations (see Richerson & Boyd 2005) or to the relative advantage of using one strategy over the other (see Kendal et al., 2005), the extent to which personal information is *ingrained* (reliably reinforced) and *preferred* might be additionally important in light of conformity processes. For instance, to induce conformity in subjects, the majority would need to represent a stronger social cue for an individual who has reached a stable behavioural pattern through frequent exposure than for an individual who has only recently learned his baseline cultural variant. Similarly, the majority would need to be more persuasive for an individual with a clear preference than for an individual who is already in doubt. Although potentially challenging to quantify, researchers should take into account this psychological distance in order to be able to interpret behavioural decisions more accurately.

4. Conclusions and future directions

Based on the considerations outlined in this review, we conclude that it is currently impossible to state whether primates' decision making is affected by the behaviour of the majority. While the reviewed studies might indicate a certain reliance on majority strategies, the reversion designs allow for too many alternative explanations to warrant interpretation of the observed behavioural patterns in terms of majority influences (cf. Claidière & Whiten, 2012). The only primate study, to our knowledge, that validly investigated majority influences reported evidence of 'majority-biased transmission' in chimpanzees, but not in orang-utans (Haun et al., 2012). In general, it is our opinion that the study of majority influences in animals, and particularly in primates, could benefit from taking into account the following considerations: First, specifying the employed operationalization and situating it within the framework proposed here would aid the cross-species comparison substantially. Moreover, it would be informative to scrutinize a species' inclination to copy the majority across both

naïve *and* knowledgeable individuals, where the assumption that naïve individuals are more likely to use social information needs to be investigated under different trade-offs (e.g. uncertain outcomes, varying acquisition costs). Second, albeit practically challenging, it would be constructive to explore more refined ways of measuring the perception records of the subjects under study. Only by knowing the subjects' observed strategy distributions can we discuss the behavioural outcomes in terms of majority influences. Third, the study of majority influences would advance by incorporating situational characteristics. Formal models have yielded different predictions based on aspects like the relative cost of individual sampling, the predictability of the environment and whether the situation requires competition or coordination to optimize fitness (Kameda & Nakanishi, 2002; Eriksson et al., 2007; Wakano & Aoki, 2007). Similarly, the instrumental and social gains of the behaviour under study are likely to influence the adaptiveness of copying the majority. By integrating these characteristics into detailed trade-off equations, we will be able to formulate more specific hypotheses about the expected form and function of the different ways in which majorities can affect behaviour. Finally, it might be worth adopting an approach in which individual differences are the subject of analysis, rather than the study group as a whole (see e.g. McElreath et al., 2005; Efferson et al., 2008). Analysis on the group level might complicate the interpretation of effects, whereas the conception that individuals might differ in their inclination to adopt the majority strategy is not inconceivable, perhaps especially not in primates.

It remains an important endeavour to single out the underlying mechanisms that drive groups to behavioural homogeneity across species. While the existence of majority influences can at most provide an indication of majority considerations in behavioural decision-making, carefully crafted designs could tease apart the plethora of mechanisms that could lead to behavioural homogeneity and assess the relative importance of actual majority preferences across a multitude of situations. Only by knowing the mechanism behind majority influences will we be able to shed light on the evolutionary roots of preferring the majority over minorities and/or personal information. Moreover, pinpointing the underlying mechanism could provide insights into species'

learning capacities given that not every mechanism bears the same potential to adaptively navigate individuals through their (changing) environments.

Acknowledgements

This work was supported by the Comparative Cognitive Anthropology research group of the Max Planck Institute for Psycholinguistics. The authors thank Katherine Cronin, Harriet Over, Rachel Kendal and three anonymous reviewers for valuable feedback on earlier drafts.

Chimpanzees flexibly adjust their behaviour in order to maximize payoffs, not to conform to majorities

Chapter 5

Based on:

Van Leeuwen, E. J. C., Cronin, K. A., Schütte, S., Call, J. & Haun, D. B. M. (2013). Chimpanzees flexibly adjust their behaviour in order to maximize payoffs, not to conform to majorities, *PLoS ONE*, 8(11), e80945.

Abstract

Chimpanzees have been shown to be adept learners, both individually and socially. Yet, sometimes their conservative nature seems to hamper the flexible adoption of superior alternatives, even to the extent that they persist in using entirely ineffective strategies. In this study, we investigated chimpanzees' behavioural flexibility in two different conditions under which social animals have been predicted to abandon personal preferences and adopt alternative strategies: i) under influence of majority demonstrations (i.e. conformity), and ii) in the presence of superior reward contingencies (i.e. maximizing payoffs). Unlike previous nonhuman primate studies, this study disentangled the concept of conformity from the tendency to maintain one's first-learned strategy. Studying captive ($n=16$) and semi-wild ($n=12$) chimpanzees in two complementary exchange paradigms, we found that chimpanzees did not abandon their behaviour in order to match the majority, but instead remained faithful to their first-learned strategy (Study 1a and 1b). However, the chimpanzees' fidelity to their first-learned strategy was overridden by an experimental upgrade of the profitability of the alternative strategy (Study 2). We interpret our observations in terms of chimpanzees' relative weighing of behavioural options as a function of situation-specific trade-offs. More specifically, contrary to previous findings, chimpanzees in our study abandoned their familiar behaviour to maximize payoffs, but not to conform to a majority.

Introduction

Contrary to current thinking (see Claidière & Whiten, 2012), we have cast doubt on the notion that nonhuman primates show conformity akin to the seminal findings in human psychology (Asch, 1956). By elucidating methodological pitfalls in the studies concerned, we have aimed to revise this notion and offer tools to improve the study of conformity in nonhuman animals (see previous chapter). In the current chapter, these suggested methodological improvements are incorporated into two empirical studies with the aim to put the notion of nonhuman primate conformity to the test more validly.

The capacity to flexibly switch between behavioural strategies might be the most critical means by which animals obtain and secure their competitive fitness advantage. Without the ability to abandon behaviour for better alternatives, animals would be dependent on the benevolence of external factors for whether they thrive or perish. Given the wide range of behavioural options available, animals are predicted to follow certain heuristics to optimize their behaviour (Kendal et al., 2009). One particular strategy that would increase an individual's competitive advantage is the optimal foraging strategy, where individuals are expected to abandon their current behavioural patterns for more beneficial alternatives in order to maximize their net payoffs (Macarthur & Pianka, 1966; McFarland, 1977). Similarly, animals may benefit from relying on the 'wisdom of the crowd', where they forgo personal strategies in order to match the strategy of the majority of group members (King & Cowlshaw, 2007). This 'conforming to majorities' can be beneficial because it allows subjects to quickly adopt locally adaptive strategies, especially in highly variable environments (Boyd & Richerson, 1985; Henrich & Boyd, 1998).

Known for their inquisitive nature, chimpanzees (*Pan troglodytes*) display a rich palette of learning behaviour, both individually (Hanus & Call, 2011; Schrauf et al., 2012; Volter & Call, 2012) and socially (Lonsdorf et al., 2004; Bonnie et al., 2007; Whiten et al., 2007). Moreover, chimpanzees display considerable between-group variation in behavioural patterns, many of which are understood in terms of social traditions (e.g. Whiten et al., 1999; Luncz et al., 2012; van Leeuwen et al., 2012). Yet, exactly how chimpanzees determine which behaviours to adopt and when to abandon their familiar practices for new ones

(e.g. when environments change or when females migrate to other communities) is largely unknown. Studies focusing on potential majority influences have indicated that chimpanzees, like humans, may discount personal information in favour of the majority strategy (Whiten et al., 2005; Bonnie et al., 2007; Hopper et al., 2011). In these studies, chimpanzees acquired one strategy socially, after which some individuals discovered the second, equally effortful strategy individually. The observation that the individual explorers reverted back to preferring the socially acquired information led researchers to conclude that chimpanzees showed ‘conformity’ (see Claidière & Whiten, 2012). However, as explained in the previous chapter, this reversion paradigm has been criticized for leaving open alternative explanations, including persevering in using first-learned strategies, and for operationalizing conformity in terms of *maintaining* instead of *abandoning* familiar behaviour. This leaves open the question whether chimpanzees would flexibly *switch* strategies under the influence of majority demonstrations (see chapter 4; also see Haun et al., 2013).

Interestingly, chimpanzees have been shown to be rather conservative in different experimental designs where switching was rewarding. When chimpanzees were faced with a new challenge, their previous knowledge either hindered the acquisition of the more optimal solution (Hanus et al., 2011; Bonnie et al., 2012), or prevented them from trying the novel (more rewarding) alternative (Marshall-Pescini & Whiten, 2008; Hrubesch et al., 2009). This relative inflexibility seemed to persist even when their familiar behaviour was made entirely ineffective (Hrubesch et al., 2009). One criticism of these studies has been that the two strategies were not always structurally identical and thus might not have been equally effortful for the chimpanzees (see Hopper et al., 2011). In conjunction, these findings beg the question of under what circumstances chimpanzees would flexibly adjust their behaviour. This question sparked our goal of evaluating chimpanzees’ relative tendency to change behaviour under conditions of i) majority influences, and ii) superior reward contingencies.

Taken together, in this study, we investigated the extent to which chimpanzees are inclined to flexibly adjust their behaviour under two different conditions. First, we aimed to test whether minority chimpanzees would

abandon their first-learned strategy for the conflicting majority strategy (Study 1). For this reason, we opted to operationalize the phenomenon of ‘conformity’ as the tendency to *forgo previous knowledge* under influence of a majority of group members demonstrating an alternative strategy (human social psychology; e.g. Asch, 1956) rather than adopting the cultural evolutionary framework where *naïve individuals* are scrutinized for their tendency to copy the majority of group members with a disproportionate likelihood (e.g. Boyd & Richerson, 1985). Moreover, for validation purposes, we applied this operationalization (see *Methods*) in two different designs in two different chimpanzee populations (Study 1a and 1b). Second, we aimed to test whether chimpanzees would abandon their first-learned strategy when an equally effortful, yet superior reward contingency was present (Study 2). This study improved on earlier designs by testing the chimpanzees in their natural social group and having two structurally identical strategies available (avoiding strategy preferences based on relative ease of execution), where the only differences between the strategies were the location and profitability (cf. Marshall-Pescini & Whiten, 2008; Hrubesch et al., 2009). Lastly, extending prior research, we tested *learned* preferences rather than pre-established food preferences (cf. Hopper et al., 2011).

Methods

Ethics Statement

Research was performed in accordance with the recommendations of the Weatherall report “The use of nonhuman primates in research” (Weatherall et al., 2006). All chimpanzees were fed a varied diet of fruits, vegetables and cereals and had ad libitum access to water. The normal diet was not restricted in this study and the chimpanzees gained extra food by participating. We certify that we have followed the rules as outlined in the ‘PASA Primate Veterinary Healthcare Manual,’ that the research adhered to the ASAB/ABS Guidelines for the Use of Animals in Research, that all animal husbandry procedures were non-invasive and that participation by the animals was voluntary. The research protocols were approved by the Max Planck Institute for Evolutionary Anthropology Ethics Committee and the Chimfunshi Research Advisory Board.

Study 1: Majority influences

Study 1 consisted of two complementary designs. In both Study 1a & 1b the chimpanzees could exchange a token for a food reward. However, Study 1a used two token types exchanged at a single location to distinguish between the majority and minority strategy, whereas Study 1b used two spatially distinct locations and one token type. By using two different experimental designs and two chimpanzee populations, we aimed to increase the validity of our study and test whether minority chimpanzees forgo their first-learned behaviour for the strategy performed by the majority of group members.

Study 1a: Wolfgang Köhler Primate Research Center

Subjects

This study was conducted at the Wolfgang Köhler Primate Research Center, Germany. The chimpanzees under study have access to an indoor (430 m²) and outdoor enclosure (4,000 m²). All enclosures include climbing structures, natural vegetation, and forms of enrichment (puzzle-boxes, jute bags, provisioning of concealed food). The group spends the nights in a series of sleeping rooms (47 m²). Subjects were 16 chimpanzees (5 males), ranging in age from 6-36 years. The trained majority consisted of 11 subjects (3 males; $M_{\text{age}} = 22.8$ years; range = 6-36 years), the minority comprised 5 subjects (2 males; $M_{\text{age}} = 17.4$ years; range = 7-35 years). The subgroups (majority and minority) were counterbalanced based on rank, age and sex as evenly as possible, except for one mother-offspring pair: mother (Ulla) and juvenile son (Kofi) were placed in the same subgroup based on recommendations from the chimpanzee keepers (both chimpanzees were allocated to the majority; see Table 1).

Table 1. Subgroups (majority and minority) in Study 1a (Leipzig) and 1b (Zambia). Individuals who actually participated during the test-sessions are designated in bold; kinship relations are indicated by matching symbols. Rank was categorized by the alpha male (“1”) and three categories (High, Middle, and Low) based on keeper reports and personal observations. The majority individuals in Zambia were the focus individuals for Study 2, where the minority strategy was upgraded in terms of rewards.

<i>Group</i>	<i>Majority</i>	<i>Rank</i>	<i>Sex</i>	<i>Age</i>	<i>Minority</i>	<i>Rank</i>	<i>Sex</i>	<i>Age</i>
Leipzig	Robert	H	male	36	Corry [*]	H	female	35
	Fraukjeⁿ	L	female	35	Sandra	M	male	18
	Ulla[*]	H	female	34	Frodo	1	female	18
	Riet ^v	H	female	34	Tai^v	M	female	9
	Natascha	M	female	31	Lobo[*]	L	male	7
	Dorien	H	female	31				
	Swela	M	female	16				
	Pia	L	female	12				
	Lome[*]	M	male	10				
	Karaⁿ	L	female	6				
	Kofi[*]	L	male	6				
Zambia	Bobby	L	male	19	Nicky	M	male	21
	Julie ^o	H	female	18	Sinky	L	male	18
	Kambo^u	L	female	16	Miracle	H	female	11
	Kathy	H	female	13	Jack^o	L	male	5
	Commander	1	male	12				
	Berta	L	female	12				
	Val	M	male	11				
	Kit^u	L	male	7				

Procedure

First, subjects were individually trained on a token-reward contingency, where the majority subjects were trained on brown, plastic sticks (Figure 1a) and the minority subjects on white, plastic cups (Figure 1b).

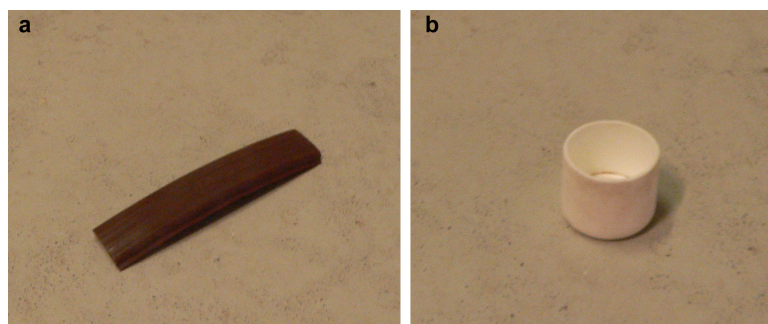


Figure 1. Depicted are the tokens that the subgroups in Study 1a were trained on: brown, plastic sticks for the majority (a), and white, plastic cups for the minority (b).

Chimpanzees were presented with a token and rewarded one piece of apple for returning it to the experimenter. After the first exchange, 6 tokens were presented on a tray in an adjacent, accessible room. The chimpanzees had to collect the tokens, travel back to the experimenter and put them through a hole in a piece of perspex that was attached to safety mesh separating the chimpanzees from the experimenter. One training session consisted of exchanging a set of 6 tokens 3 consecutive times and lasted an average of 12.4 minutes (range 6.7 – 19.3 minutes). All chimpanzees were trained on their respective token for one session on three days over the course of two weeks, and returned all tokens successfully.

Second, individuals were trained in their indoor enclosure with only their respective subgroup (majority/minority) present. For the first four sessions (one hour each, one per day), the human experimenter sat behind the safety mesh (the 'exchange station') and a token dispenser (containing only the trained token) was attached on the same mesh. The dispenser was made out of perspex and was continuously, automatically refilled. Chimpanzees could freely obtain tokens from the dispenser. For four subsequent sessions (one hour each, one per day), the dispenser was moved to a location approximately 30 meters from the exchange station. Throughout these eight training sessions, eight majority and two minority individuals participated, with each individual exchanging at least 20 tokens per session. Participation may have been less in these training sessions due to the increase in physical and social distractions compared to individual training.

During testing, both tokens (sticks and cups) were available at one location in the enclosure (from two dispensers, each containing one type of token) and rewarded equally (one piece of apple per token) upon delivery at the exchange station (see Figure 2a).

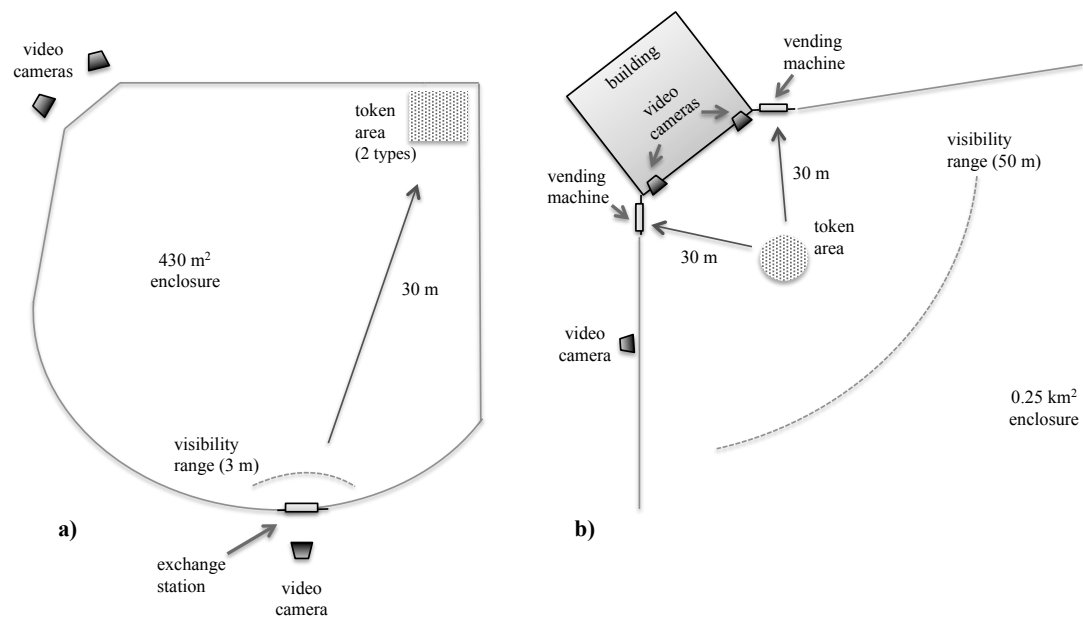


Figure 2. Schematic overview of the experimental setup in Study 1a, Leipzig Zoo (a) and Study 1b and 2, Chimfunshi Wildlife Orphanage Trust (b).

Chimpanzees were tested for one hour on ten consecutive days in March 2012 (one week after training). All sessions were recorded using JVC GY-HM100U HD video cameras from three vantage points. Auditory commentary was provided on one of the JVC cameras by the experimenter (detailing which chimpanzee exchanged which token type). Auditory comments were subsequently used to extract information on the 'token exchanges', the videos were analysed for obtaining the 'perception records', i.e. for each individual within a 3-meter radius of the exchange station and being oriented towards the exchange station, we identified which other individuals were exchanging tokens and which type of token they used. This information amounted to individual scores of the number of times the majority and minority token had been observed to be used in exchanges, and the number of different subjects that were observed to use the two different token types. Whereas all tokens were equally rewarded upon exchanging, only the token exchanges where the individual had collected the token at the dispenser ($n=2102$) were included in the first analysis investigating the effect of majority demonstrations on the behaviour of minority chimpanzees; tokens that had been stolen from others ($n=103$) were considered opportunistically collected instead of chosen. A second analysis including all

tokens (collected from dispenser and stolen, $n=2205$) was performed to investigate whether the pattern of results would differ.

Study 1b: Chimfunshi Wildlife Orphanage Trust

Subjects

This study was conducted at the Chimfunshi Wildlife Orphanage Trust, a sanctuary that houses more than a hundred chimpanzees under close to natural conditions in the north-western part of Zambia (for details, see van Leeuwen et al., 2012). The chimpanzees under study (Group 4) live in a 0.25 km² enclosure of Miombo forest (Ron & McGrew, 1988). The chimpanzees spend all their time outside (including the nights), except for one 2-hour food-provisioning session per day, during which they receive additional fruits and vegetables in their indoor holding facility. Subjects were 12 chimpanzees (6 males), ranging in age from 4-21 years. The majority comprised 8 chimpanzees (3 males; $M_{\text{age}} = 13.0$ years; range = 4-18 years), the minority 4 chimpanzees (3 males; $M_{\text{age}} = 14.8$ years; range = 7-21 years). The subgroups (majority and minority) were counterbalanced based on rank, age and sex as evenly as possible (see Table 1).

Procedure

First, chimpanzees were individually trained on a token-reward contingency, where chimpanzees received one peanut for putting a wooden ball ($\varnothing=3.0\text{cm}$) through a hole in a piece of perspex that was attached to the mesh of their indoor holding space. At this stage, the balls were first handed to the chimpanzees and imitations of chimpanzee vocalizations were used to engage the chimpanzees. After the chimpanzees engaged readily, we threw the balls into their holding space and tested whether they would participate. Ten individuals (7 majority, 3 minority) reached the criterion of returning 10 balls through the hole in the perspex on at least three days; the remaining two individuals did not participate and were not included in the study.

Second, subjects were trained in their outdoor enclosure with only their respective subgroup (majority/minority) and one vending machine present. During this subgroup training, the other subgroup remained inside the building

without a clear view on the side where the other subgroup was being trained as to prevent any social learning from happening prior to testing. The vending machines comprised a perspex construction (75 x 45 x 32 cm) supporting an automated food-dispenser with a metal front (painted as two Zambian bakeries: 'Princes Bakery' for the majority, 'G&G Bakery' for the minority; see Figure 3).



Figure 3. Depicted are the vending machines used in Study 1b and Study 2: The Plexiglas structure with the automated peanut dispenser (a), and the painted metal frames with the corresponding holes for the wooden balls (hole Y) and the food rewards (hole X). The “Princes Bakery” (b) and the “G&G Bakery” (c) were the trained strategies for the majority and minority, respectively, where the latter was upgraded in Study 2.

The machines were attached to safety mesh such that the chimpanzees could view the uniquely painted metal front; each front had an upper hole for token insertion and a lower hole to dispense food. Initially, an experimenter provided one piece of food through the lower hole of the machine after the chimpanzee had inserted a ball through the upper hole, later an automated device dispensed the food and the experimenter remained over 10 meters away. Nine individuals (6 majority) reached the criterion of exchanging 10 balls on at least three days.

We tested the entire social group in their outdoor enclosure for one hour on ten consecutive days in April 2012 (one week after training), during which both vending machines were available at approximately 20 meters from each other (see Figure 2b). Importantly, and contrary to the token design of Study 1a, we used this ‘spatially-distinct strategies design’ in order to make it easier for the subjects to observe which strategies the other subjects were using. For the first six days, both vending machines were operational, yielding one peanut per ball

automatically. Due to machine malfunctioning, during the final four testing days, experimenters manually controlled food dispensation through the machines (without being visible to the chimpanzees). The experimenters rewarded upon the audible click of a ball entering the vending machine and were not able to monitor the behaviour of the chimpanzees. Balls were thrown to the subjects in a randomized order (using a random name selection procedure without replacement) at a predefined distance of approximately 30 meters from each vending machine, with 1 or 2 balls per throw. Deviation from the randomized order sometimes occurred (e.g. when subjects were not present). Once a chimpanzee obtained one or more balls, the experimenter would wait for this individual to exchange the ball(s) and leave the vending machine before targeting another individual. This procedure was adopted to increase the likelihood that chimpanzees could choose between the vending machines without one of them being occupied by another individual. All sessions were recorded using JVC GY-HM100U HD video cameras from three vantage points. Auditory commentary was provided on one of the JVC cameras by the experimenter, detailing which chimpanzee exchanged at which vending machine and whether either machine was occupied by another individual. Auditory comments and videos were subsequently used to extract information on the 'token exchanges', videos were analysed for obtaining the 'perception records', i.e. the focal individual's presence within visibility range (within 50 meters from the vending machines; see Figure 2b), while being oriented towards the participating subject(s). Whereas all balls were equally rewarded upon insertion in the vending machines, only the exchanges that occurred when neither vending machine was occupied by another individual ($n=413$) were used for the analysis of whether the minority chimpanzees adjusted their behaviour to the majority for the reason that we were interested in the chimpanzees' free strategy choices (not biased by the social inaccessibility of one of the vending machines). However, similar to Study 1a, in a subsequent analysis, we additionally used the full dataset ($n=861$) in our analysis of the behaviour of the minority chimpanzees.

For establishing the perception records, since exchanges could be visible regardless of whether the tokens were collected or stolen (Study 1a) or whether

one or two vending machines were occupied (Study 1b), all exchanges were included (Study 1a: $n=2205$; Study 1b: $n=861$). All analyses were two-tailed unless indicated differently.

Results

All chimpanzees, both in the majority and minority, preferred to use their trained strategy over the course of 10 test days, both in Study 1a and 1b (one-sample Wilcoxon signed rank test against 50% (no preference for either strategy), Study 1a: $W=2.82$, $n=10$, $p=0.005$, median = 86.8%, range = 31.1 – 100%; Study 1b: $W=2.71$, $n=9$, $p=0.007$, median = 100%, range = 77.8 – 100%).

Focusing in on the chimpanzees in the minorities, we found no evidence for conformity in either chimpanzee population. While the perception records indicated that the minority chimpanzees more often observed chimpanzees using the majority strategy compared to the minority strategy, both in absolute frequency (regardless of which individual was exchanging) and in the number of unique individuals (see Figure 4), they remained faithful to their trained strategy with high fidelity ($W=2.06$, $n=5$, $p=0.039$; Figure 4), both in Study 1a ($n=2$, median = 99.1%, range = 67.9 – 100%, token exchanges per individual per day $M = 38.7$) and Study 1b ($n=3$, median = 100%, range = 33.3 – 100%, free exchanges at the vending machines per individual per day $M = 8.7$).

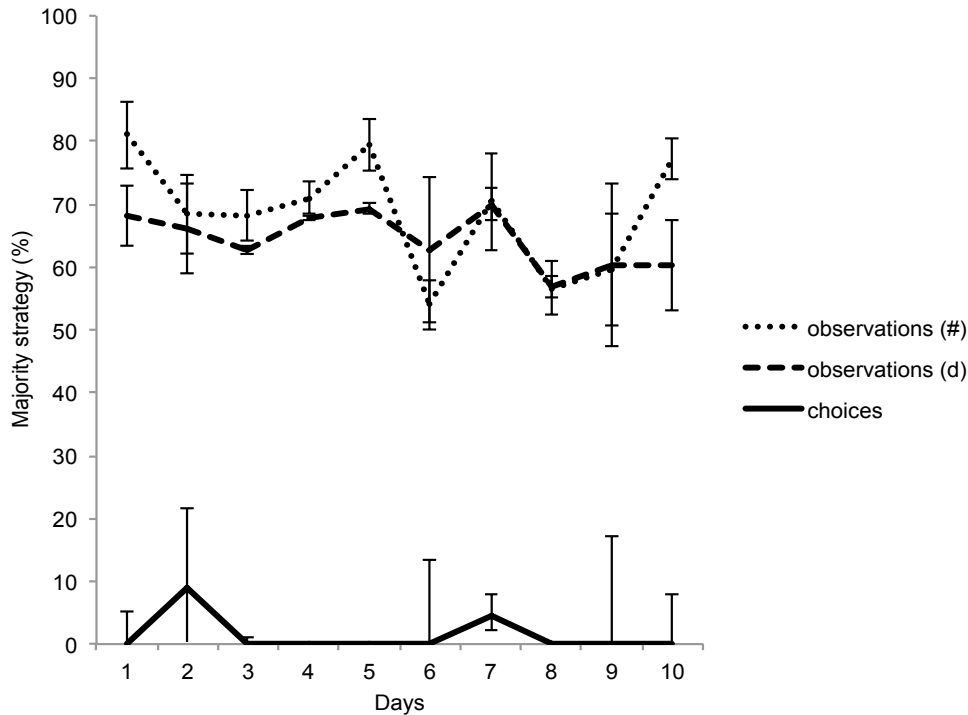


Figure 4. Mean (\pm s.e.m.) percentage by which the minority chimpanzees of Study 1 ($n=5$) *observed* majority strategy demonstrations, both in absolute frequencies (#) and in number of unique demonstrators (d), supplemented with the median percentages (with the lower and upper error hinge representing the first and third quartile, respectively) by which the minority chimpanzees *chose* to use the majority strategy per day (Exp. 1a: mean choices per individual per day = 39.9 token exchanges, range 38-103; Exp. 1b: mean choices per individual per day = 11.4 exchanges at the vending machines, range 7-23).

Analysis of all choices made by the minority chimpanzees (thus, including stolen tokens in Study 1a and location choices where one vending machine was already occupied by another chimpanzee in Study 1b) yielded similar results (fidelity to trained strategy: $W=2.03$, $n=5$, $p=0.042$), both in Study 1a (median = 98.8%, range = 68.8 – 100%) and 1b (median = 100%, range = 0 – 100%).

Study 2: Superior reward contingencies

Subjects & Procedure

Here, we investigated chimpanzees' strategy use within an unequal reward paradigm. While employing the same procedure as in Study 1b – with the same individuals at the Chimfunshi Wildlife Orphanage Trust (Zambia) – the chimpanzees could now choose between a machine that yielded the same reward

as in Study 1b (1 peanut/ball) or the alternative machine that yielded 5 peanuts/ball. Because this study was designed to test whether chimpanzees would change their behaviour upon the introduction of a superior alternative strategy, we maximized the number of individuals in our sample by upgrading the vending machine that was previously used by the least number of individuals ('G&G Bakery'). In other words, we aimed to investigate the behaviour of the chimpanzees that had been in the majority in Study 1b ($n=6$), leaving the minority chimpanzees of Study 1b ($n=3$) out of this sample. The chimpanzees were tested for 1 hour per day on 10 consecutive days (immediately following the end of Study 1b). Again, all exchanges were rewarded based on the predefined reward-paradigm (1 peanut/ball at 'Princes Bakery' and 5 peanuts/ball at 'G&G Bakery'). All sessions were recorded using JVC GY-HM100U HD video cameras from three vantage points. Videos were subsequently analysed for 'vending machine choices', where the choices of the chimpanzees who had a pre-existing preference for the machine that continued to provide a single reward were central to the analysis. In a first analysis, for the same reason as in Study 1b, only the exchanges where no machine was occupied ($n=321$) were used and a subsequent analysis included all exchanges ($n=416$). All analyses were two-tailed unless indicated differently.

Results

Upon upgrading the alternative strategy, the majority chimpanzees of Study 1b started switching their strategy (see Figure 5), leading to a significant change of their preferences when comparing the 10 testing days of Study 1b to the subsequent 10 testing days in Study 2 (related-samples Wilcoxon signed rank test: $Z = -2.02$, $n=6$, $p=0.043$, $\text{median}_{1b} = 100\%$, $\text{median}_2 = 37.8\%$).

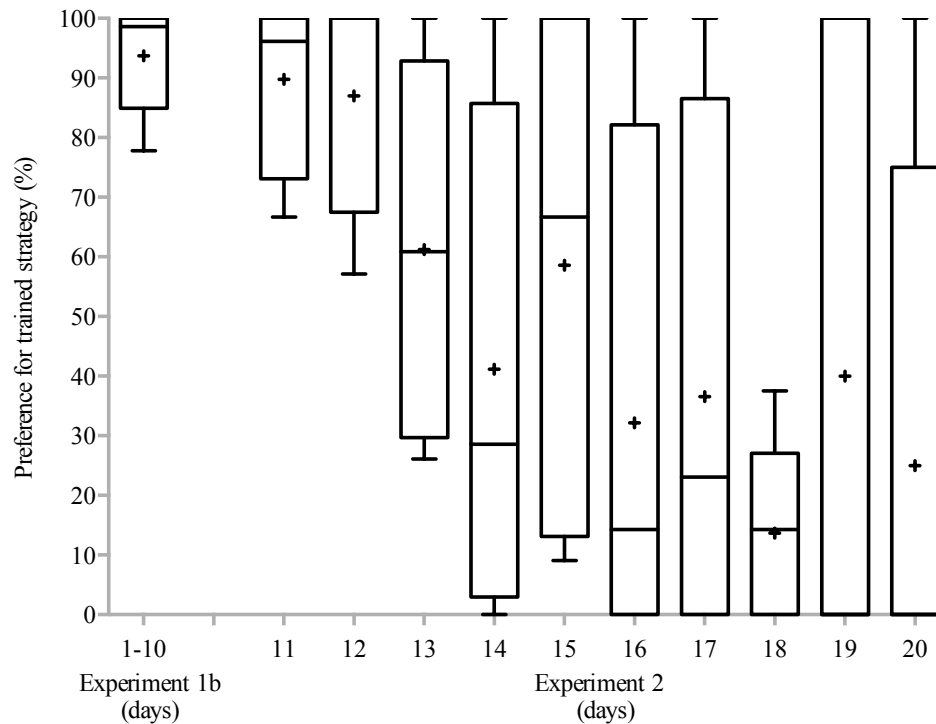


Figure 5. Median (with the lower and upper boxplot hinge representing the first and third quartile, respectively, and the crosses within the boxplots representing the means) preference for the trained strategy of the majority chimpanzees in Zambia throughout Study 2. Data point at time point “1-10” represent the median preference of the majority chimpanzees for the trained strategy over the first 10 days (Study 1b). Data points at time points 11 to 20 refer to the median preferences for the trained strategy (i.e. the least productive) in the ‘superior reward contingency’ design (Study 2).

The same results were obtained when analysing all exchanges, including the ones where one or both of the vending machines were already occupied by another chimpanzees ($Z = -2.02$, $n = 6$, $p = 0.043$, $\text{median}_{1b} = 100\%$, $\text{median}_2 = 41.6\%$). On the individual level, comparing the last session of Study 1b (henceforth ‘T1’) to the last session of Study 2 (henceforth ‘T2’), three chimpanzees had significantly changed their preference from their familiar strategy to the upgraded strategy (one-tailed Fisher exact tests with in subscript the choices for the trained and not-trained strategy, respectively: *Individual 1*: $T1_{6,0}$ $T2_{3,15}$ $p < 0.001$; *Individual 2*: $T1_{17,0}$ $T2_{0,12}$ $p < 0.001$; *Individual 4*: $T1_{9,0}$ $T2_{1,6}$ $p < 0.001$; Bonferroni-Holm corrected p -value = 0.008; Figure 6).

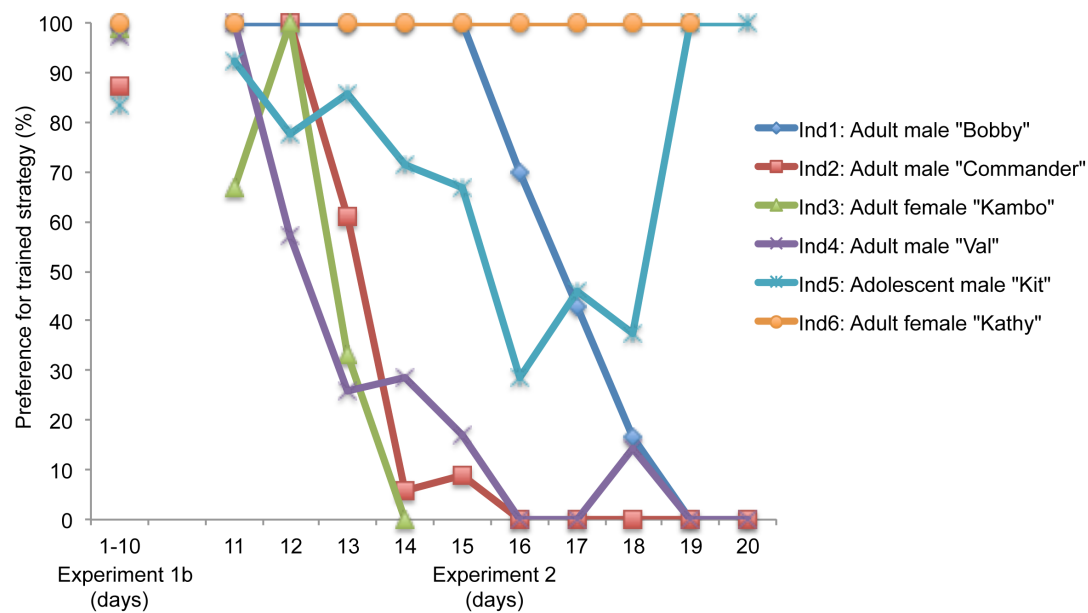


Figure 6. Individual preferences for the trained strategy of the majority chimpanzees in Zambia throughout Study 2. Data points at time point “1-10” represent the average preferences for the trained strategy over the first 10 days per individual (Study 1b). Data points at time points 11 to 20 refer to the individual preferences for the trained strategy (the least profitable) compared to the non-trained strategy (the most profitable).

Regarding the remaining chimpanzees: *Individual 3* started using the upgraded strategy (see Figure 6), where her behavioural choice on the last day that she engaged in the study indicates that she switched from her trained strategy to the upgraded strategy (day4_{0,1}). However, due to absence of participation after day 4, no standardized analysis could be done. *Individual 5* did not switch strategies (T1_{5,0} T2_{4,0} $p=1.0$). However, this 7-year old male started switching strategies until day 8 (comparing T1_{5,0} to day8_{2,5} : $p=0.027$; Bonferroni-Holm corrected p -value=0.025), after which he reverted back to his trained strategy (see Figure 6). *Individual 6* never used the upgraded strategy (T1_{8,0} T2_{6,0} $p=1.0$; see Figure 6). Importantly, there was no indication that the strength by which these six chimpanzees had experienced their first-learned strategy throughout the preceding conformity study (Study 1b) related negatively to their switching behaviour in this upgraded paradigm: For instance, the two individuals that switched relatively quickly (Ind. 2 and 4; see Figure 6) had the most personal experience with their first-learned strategy in the conformity study (84 and 105 exchanges respectively; average across individuals = 46 exchanges), while they observed the usage of their first-learned strategy roughly as much as the other

chimpanzees under scrutiny (312 and 336 exchanges respectively; average across individuals = 316 exchanges). The female that never switched in the upgraded paradigm (Ind. 6; see Figure 6) had an average experience with her first-learned strategy throughout the conformity study, both personally (53 exchanges) and socially (328 exchanges).

General Discussion

In this study, we investigated two possible conditions under which chimpanzees might flexibly adjust their familiar behaviour by sequentially exposing them to conflicting majority influences and superior payoff alternatives. When tested in the presence of a majority of individuals using an alternative, equally beneficial strategy, chimpanzees remained faithful to their first-learned strategy with high fidelity. However, when the chimpanzees' strategy was made relatively inefficient by upgrading the yield of the alternative strategy, chimpanzees tended to forgo their first-learned strategy in favour of the more productive strategy. In conjunction, these results indicate that chimpanzees adjust their behaviour conditionally. In this study, where chimpanzees did not change their behaviour in order to conform to the majority of group members, the inclination to maximize personal benefits drove chimpanzees to adjust their behaviour. These findings stand in contrast to some recent social learning and conformity studies (Marshall-Pescini & Whiten, 2008; Hrubesch et al., 2009; Hopper et al., 2011; but see Dean et al., 2012; Yamamoto et al., 2013).

Notably, the current study may provide an alternative explanation for the observation that chimpanzees tended to revert back to their first-learned strategies after discovering an equally or even more rewarding alternative strategy in previous studies (Whiten et al., 2005; Bonnie et al., 2007; Hopper et al., 2011). In these studies, the behavioural pattern of reverting back to using the first-learned strategy was interpreted in terms of conformity (also see Claidière & Whiten, 2012), even for reasons of "aiding social cohesion and the maintenance of group dynamics" (Hopper et al., 2011, p. 6). Hopper and colleagues (Hopper et al., 2011) interpreted the behaviour of the chimpanzees in their study as 'normative conformity', a term coined by Deutsch and Gerard (Deutsch & Gerard, 1955) to distinguish conformity based on the desire to create

or maintain a positive group sense (normative conformity) from conformity based on the aim to obtain the most fitting strategy in a given environment (informational conformity) (Deutsch & Gerard, 1955). However, in their study (Hopper et al., 2011; but also see Whiten et al., 2005; Bonnie et al., 2007), the conformity strategy coincided with the strategy to persevere in first-learned practices, which makes the conclusion that the chimpanzees were conformists in the first place premature. The present study shows that chimpanzees remain faithful to their first-learned strategy, even when it is not the strategy used by most group members, which is indicative of a conservative tendency rather than conformity (van Leeuwen & Haun, 2013). The fact that chimpanzees have been shown to be sensitive to majority demonstrations when acquiring *novel* behaviour (Haun et al., 2012) indicates that although the majority may represent a vector in the decision-making process of chimpanzees, it does not necessarily provide a strong enough incentive to make them change their behaviour. Moreover, in this study by Haun and colleagues focusing on majority influences in the context of acquiring novel behaviour (see Haun et al., 2012), the most likely explanation in motivational terms would be that the chimpanzees use the demonstrations to obtain knowledge about their environment (informational conformity), as they were not exposed to any group pressure nor tested with conspecifics present (necessary conditions to tap into any form of normative conformity). In light of the absence of conformity in our paradigm where we exposed *knowledgeable* individuals to majority demonstrations, it would be interesting to titrate the effects of increasingly large (relative) majority sizes on chimpanzees' tendencies to persevere in their first-learned behaviour, especially in relation to first-learned strategies with different magnitudes of familiarity and/or preference (see van Leeuwen & Haun, 2013).

However, the chimpanzees in the present study were not invariably conservative. Instead, most chimpanzees (5/6) showed some evidence of at least trying the alternative strategy when it was upgraded to yield a 5-fold reward compared to their first-learned strategy, with at least half of them converging on this more profitable strategy. Although impossible to quantify the force of the number of demonstrators in comparison to the force of the net increase in the number of peanuts, these findings seem to indicate that for chimpanzees

maximizing personal gains provides a stronger motivation to adjust behaviour than matching the majority. Contrary to previous studies showing that chimpanzees did not readily switch to more efficient or rewarding strategies (e.g. Marshall-Pescini & Whiten, 2008; Hrubesch et al., 2009), this upgrading behaviour matches the predictions from optimal foraging theory, where animals are expected to gradually adjust their foraging behaviour based on the net payoffs of their endeavours (Macarthur & Pianka, 1966; McFarland, 1977). In line with theoretical predictions about the usage of social learning strategies (Boyd & Richerson, 1985; Laland, 2004), the chimpanzees could also have employed a selective *copy-if-better* strategy (Schlag, 1998; Laland, 2004). Although our study was not designed to distinguish between specific optimization heuristics (see Schlag, 1998; Laland, 2004), the chimpanzees central to Study 2 could have copied the behavioural choices of the chimpanzees that were trained on the upgraded location (the three minority subjects from Study 1b) and who were thus rewarded substantially more for exchanging a token. In support of this explanation is the observation that some individuals who upgraded during Study 2 had never tried that vending machine when the payoffs were equal. This might indicate that social demonstrations of the greater efficiency of the alternative strategy (e.g. in form of prolonged presence, food grunting or indirect cues like increased amounts of peanut shells) in the second study were necessary for the chimpanzees to switch strategies. The underlying mechanism could have been relatively simple, where local enhancement and response facilitation would have directed the chimpanzees towards the more efficient strategy. Alternatively, the chimpanzees could have discovered the better strategy by individual exploration. In a follow-up study it would be informative to include a condition in which there is no social reference to the better strategy in order to draw conclusions on the mechanism underlying the behavioural upgrading.

One of the switching chimpanzees, however, radically reverted back to his first-learned strategy (i.e. the least productive one) during the last two days of Study 2 (Individual 5; see Figure 6). Albeit counterintuitive, we found indications that this strategy was a payoff-maximizing strategy for this low-ranking individual. Specifically, this individual was the youngest and lowest ranking individual that switched to the most profitable strategy, which caused him to be

at risk of losing his peanuts to the more dominant individuals. Together with one young, low-ranking individual that was trained to use the strategy that was upgraded in Study 2, this switching individual was the only one who started to get harassed by others as of day 7 of Study 2 (which was reflected in quick approaches when the low-ranking individuals were getting close to the profitable vending machine, not in theft of the distributed tokens). Since the more profitable vending machine rewarded five peanuts instead of one, there was more time for the dominant individuals to approach these low-ranking individuals after they had inserted a ball in the vending machine and still be successful at stealing one or more rewards. Over time, this pattern of behaviour appeared to cause both these low-ranking individuals to solely use the least profitable vending machine, which in case of individual 5 meant a reversion back to using his first-learned strategy.

In sum, the knowledgeable state of the individuals in our first study (i.e. being trained on one of the two equally effortful strategies) allowed us to pit chimpanzees' conservative disposition (Marshall-Pescini & Whiten, 2008; Hrubesch et al., 2009) against their postulated tendency to adopt majority strategies (Whiten et al., 2005; Hopper et al., 2011). Using two complementary designs in which we disentangled the tendency to persevere in using first-learned strategies from conformity and verified that minority chimpanzees actually perceived conflicting social information from the majority of group members (see van Leeuwen & Haun, 2013), this study indicates that chimpanzees may not readily conform to majorities, contrary to previous claims (Whiten et al., 2005; Hopper et al., 2011; Claidière & Whiten, 2012). In contrast, in the second study, the increased efficiency of the alternative strategy did induce behavioural adjustment in the chimpanzees, which seems to indicate that chimpanzees are more inclined to abandon familiar behaviour for reward maximizing heuristics than for majority biased heuristics. Moreover, the observation that chimpanzees discard ingrained behavioural patterns for better alternatives (this study) calls into question the argument that chimpanzees lack cumulative culture owing to their conservative nature (see Mesoudi, 2011). This questioning is supported by recent evidence showing that chimpanzees continued exploring a puzzle-box after mastering a reliably rewarding strategy

(Dean et al., 2012), and upgraded their first-learned straw-handling technique ('straw-dipping') after observing a conspecific using the more efficient 'straw-sucking' technique in a juice-foraging task (Yamamoto et al., 2013).

Importantly, we note that our studies are inevitably limited in their generalizability. For instance, the selection pressures in a wild setting may place much higher incentives on conforming to the majority of the group than in a setting where the chimpanzees are being provisioned. In a similar vein, the reason why the chimpanzees in our study did upgrade to more profitable strategies (while they have been shown to be reluctant to upgrade in other studies) might be explained by specific characteristics of our study designs. For instance, in our study, the chimpanzees could easily perceive the more profitable strategy because the strategies were spatially separated (cf. Hopper et al., 2011). Additionally, they were tested within their social group, which may provide a more relaxed learning environment for chimpanzees than in observation rooms separated from their group (cf. Marshall-Pescini & Whiten, 2008). Also, the chimpanzees in our studies used behaviours that were similar across subgroups: only the token-type (Study 1a) and the location of exchange (Study 1b) differed between individuals, not the actual technique of performance. It could be the case that chimpanzees respond differently to majority influences and superior reward contingencies when the conflicting strategies comprise structurally different techniques, as seems to be indicated by their tool use- and social custom convergence (Luncz et al., 2012; van Leeuwen et al., 2012, respectively), and the relative absence of upgrading behaviour when the more profitable strategy comprises learning a new technique (Marshall-Pescini & Whiten, 2008; Hrubesch et al., 2009). Similarly, it would be interesting to investigate to what extent the process by which the first strategy was acquired affects chimpanzees' tendency to adopt better alternatives: Where the chimpanzees in our study had learned their first strategy by means of individual learning, the chimpanzees in the conformity study by Hopper and colleagues had learned their first strategy socially (Hopper et al., 2011). It might be possible that chimpanzees are more flexible with individually-acquired information than with information that was obtained by observing conspecifics, which seemed to be demonstrated in a study by Price and colleagues, where chimpanzees who had learned to use a raking tool

socially were adjusting the tool less efficiently than the chimpanzees who had discovered the use of the tool by themselves (Price et al., 2009).

In this study, we found chimpanzees to be more motivated to maintain their first-learned strategy than to conform to the majority of group members. This finding confirms our methodological concerns expressed in chapter 4 and shows that first-learned behaviours, or primacy effects, can be a potent force in shaping chimpanzees' decision-making processes, perhaps similar to what could be found in humans (i.e., habit formation and conservatism). The presence of a superior alternative, however, did sever the chimpanzees' fidelity to their first-learned strategy, indicating that chimpanzees selectively adjust their behaviour, given the right kind of incentive. Taken together, these findings demonstrate that chimpanzees, albeit sensitive to social influences in many contexts, weigh their own knowledge and experience heavily in the process of decision making. Exploring the bifurcation points in animals' learning dynamics is an exciting endeavour and continues to be a fruitful enterprise for gaining insights in species-specific behaviour, the extent to which learning biases are distributed across taxa, and which selection pressures might have given rise to their existence.

Acknowledgements

The authors thank the Zambia Wildlife Authority, and the staff and chimpanzee caretakers of the Wolfgang Köhler Primate Research Center and the Chimfunshi Wildlife Orphanage Trust for facilitating the research. A special thank you to Patrick Mwika, Marloes van der Goot, Peggy Albers and Ian Ferreira for their elaborate assistance throughout data-collection, and we thank Rick van Viersen and the Technical Group of the Max Planck Institute for Psycholinguistics for their technical assistance. We are very grateful to Rachel Kendal and one anonymous reviewer for helpful comments on an earlier version of this paper.

Conformity without majority? The case for demarcating social from majority influences

Chapter 6

Based on:

Van Leeuwen, E. J. C., & Haun, D. B. M. (2014). Conformity without majority? The case for demarcating social from majority influences. *Animal Behaviour*, 96, 187-194.

Abstract

In this review, we explore the extent to which the recent evidence for conformity in nonhuman animals may alternatively be explained by the animals' preference for social information regardless of the number of individuals demonstrating the respective behaviour. Conformity as research topic originated in human psychology and has been described as the phenomenon where individuals change their behaviour towards matching the behaviour that is displayed by the majority of group members. Recent studies have aimed to investigate the same process in nonhuman animals, however, most of the adopted designs have not been able to control for social influences independent of any majority influence and some studies have not even incorporated a majority in their designs. This begs the question to what extent the 'conformity interpretation' is preliminary and should be revisited in light of animals' general susceptibility to social influences. Similarly, demarcating social from majority influences sheds new light on the original findings in human psychology and motivates reinterpretation of the reported behavioural patterns in terms of *social* instead of *majority* influences. Conformity can have profound ramifications for individual fitness and group dynamics; identifying the exact source responsible for animals' behavioural adjustments is essential for understanding animals' learning biases and interpreting cross-species data in terms of evolutionary processes.

Introduction

Following up on the investigation of conformity principles in chapter 4 and 5, in the current chapter, the focus will be on the majority aspect of conformity. Previous considerations have mainly dealt with offering alternative explanations for the purported conformity findings in nonhuman primates in the form of primacy effects and conservatism (see chapter 4). Here, with the same aim of optimizing conformity research, both human and nonhuman animal studies will be assessed in light of another alternative explanation for the conformity findings: social influence.

Dating back to 1932, when Arthur Jenness observed that individuals' estimates of the number of beans in a jar were considerably influenced by the estimate of the majority of group members (Jenness, 1932), conformity has received extensive attention in human psychology. Defined by altering opinions or behaviour in order to match the majority, subsequent research robustly showed that a surprising number of the adult participants are conformists, even when the majority stance is conspicuously erroneous (Asch, 1956; Bond & Smith, 1996; Sherif, 1936). In later years, it was shown that opting for the majority stance does not represent a biological conundrum, but may instead bestow substantial fitness benefits (Henrich & Boyd, 1998; King & Cowlshaw, 2007; Richerson & Boyd, 2005; Wolf, Kurvers, Ward, Krause & Krause, 2013).

The tendency to adopt the behaviour of the majority of group members is considered to be one of the driving forces behind cultural diversification (Boyd & Richerson 1985; Henrich & Boyd 1998). By converging on the most prevalent conventions, groups move towards behavioural homogeneity while at the same time increasing the likelihood of emergent between-group heterogeneity: the hallmark of culture (Richerson & Boyd 2005). In recent years, majority influence has become a favourable research topic for behavioural biologists. One line of research has focused on our closest living relatives, the nonhuman primates (chimpanzees, *Pan troglodytes*: Bonnie, Horner, Whiten, & de Waal, 2007; Haun, Rekers, & Tomasello, 2012; Hopper, Schapiro, Lambeth, & Brosnan, 2011; Whiten, Horner, & de Waal, 2005; capuchin monkeys, *Cebus apella*: Dindo, Thierry, & Whiten, 2008; Dindo, Whiten, & de Waal, 2009; Perry, 2009), which could enable intriguing analysis of the evolutionary roots of this human

phenomenon (MacLean et al., 2012). Another line of research has aimed to investigate the possibility of convergent evolution of conformity by focusing on phylogenetically more distant species, such as fish (Day, MacDonald, Brown, Laland & Reader, 2001; Kendal, Coolen, & Laland, 2004; Pike & Laland, 2010), rats (Galef & Whiskin, 2008; Jolles, de Visser, & van den Bos, 2011; Konopasky & Telegdy, 1977) and fruit flies (Battesti, Moreno, Joly & Mery, 2012). However, as we aim to show in this review, most studies in both lines of investigation seemed to have overlooked the distinction between social and majority influences.

Specifically, in this review, we evaluate relevant conformity studies across animal taxa (including humans) to show that most designs have been insufficiently accurate to pinpoint whether subjects' behavioural adjustment was caused by social or majority influences. Important to note here is the logical distinction between social and majority influences: although majority influence is inevitably social influence, behavioural adjustment caused by social influences need not be caused by majority influence. For instance, individuals could discard their personal preference by copying alternative behaviour from just one other individual, as opposed to the majority of individuals. This distinction would need to be taken seriously if conformity, defined by not just social but majority influence, is to be studied validly. For this reason, first, we review recent conformity findings across nonhuman animals (henceforth 'animals') in light of the distinction between social and majority influences. Second, we revisit the essential details of the human psychology studies that gave rise to the conformity definition and explore whether their findings could be explained in terms other than majority influence. Lastly, we conclude with suggestions to translate the definitional distinction between social and majority influences into empirical study designs. To be able to interpret the intriguing social phenomenon of 'conformity' in evolutionary terms, or identify the exact learning mechanisms present in species' behavioural repertoires, we need to calibrate the conformity designs across research disciplines.

To avoid confusion, it is important to explicitly distinguish between the conformity definitions that emerged from the study of human psychology and cultural evolution (see Morgan & Laland, 2012; also see chapter 4). The human psychology definition emphasizes the fact that individuals have to forgo their

behavioural inclination, thereby adopting the behaviour of the majority (e.g., Asch, 1956; Jenness, 1932; Sherif, 1936). Thus, in this case, individuals possess a certain behaviour or conviction before being exposed to the conflicting stance of the majority. The cultural evolutionary approach, by contrast, investigates cost/benefit scenarios in which it would be beneficial (in terms of fitness consequences) for individuals to learn socially instead of individually, and has shown that in many cases where individuals are predicted to learn socially, they would favour not just any social information, but the information specifically transmitted by the majority of interactants (Boyd & Richerson, 1985; Henrich & Boyd, 1998; also see Aoki & Feldman, 2013). In other words, the cultural evolutionary approach analyses individuals on the verge of obtaining their first behavioural strategy, not individuals discarding their familiar behaviour. Thus, where the psychological approach to conformity focuses on the determinants of knowledgeable individuals' tendency to adjust their behaviour to the majority, the cultural evolutionary approach typically models the likelihood of naïve individuals obtaining the most common cultural variant. This subtle distinction could have important ramifications for understanding behavioural patterns indicative of conformity: where individuals in possession of a functional and/or preferred behavioural strategy might be more inclined to persevere in using their strategy than adopting random social information, individuals that are already predicted to learn socially could end up with the majority behaviour through exactly this process of random copying (e.g. see Mesoudi, 2009). We elaborate on this distinction in the section on human conformity findings. Furthermore, while the human psychology approach has traditionally been more concerned with immediately influential variables such as group size and task ambiguity (e.g. see Bond 2005), the cultural evolutionary approach has mainly been concerned with the broader ramifications of behavioural decisions for the evolution of culture, expressed as relative within-group homogeneity and between-group heterogeneity (e.g. see Richerson & Boyd, 2005). For the reason that we are interested in the extent to which conformity can be identified through specific experimental features (i.e. the manipulation of group size) and dissected in social and majority influences, in this review we focus entirely on the human psychology operationalization of conformity.

DO PRIMATES SHOW CONFORMITY?

Most studies on conformity in animals have been conducted in nonhuman primates (henceforth 'primates'). On the one hand, the label 'conformity' has been used to describe the process by which primates obtain the strategy that gradually becomes the majority strategy. Starting with one skilled individual (natural invention or trained skill), the rest of the group acquires the same particular way of behaving by means of social learning (Hopper et al., 2011; Perry, 2009; Whiten et al., 2005). On the other hand, as described in detail in chapter 4, the label 'conformity' has been used to describe the process by which primates would revert back to the majority strategy after discovering an alternative strategy (chimpanzees: Bonnie et al., 2007; Hopper et al., 2011; Whiten et al., 2005; capuchin monkeys: Dindo et al., 2008; Dindo et al., 2009). Here, after socially acquiring a particular way of behaving, some individuals would occasionally explore an alternative strategy, but then change back to using c.q. 'preferring' the majority strategy. The interpretation of this latter behavioural pattern in terms of conformity has been criticized based on the fact that the same behavioural pattern could be explained by conservatism (i.e. the reluctance to switch techniques once one technique has been proficiently mastered; Hrubesch, Preuschoft, & van Schaik, 2009; Pesendorfer et al. 2009; van Leeuwen, Cronin, Schütte, Call, & Haun, 2013; van Leeuwen & Haun 2013). In that case, the re-convergence to the majority behaviour might not even be socially mediated (see van Leeuwen & Haun, 2013). More relevant to the current focus, however, are the following issues.

First, in the case where conformity was claimed based on gradual behavioural convergence (e.g. Hopper et al., 2011, p. 6), for at least half of the group members there could not have been a majority present to conform to. In other words, for the first half of the group members, this gradual diffusion of information over individuals cannot possibly be attributed to conformity as it is typically defined. The second half of naïve learners could technically have been influenced by the majority (if all individuals of the first half adopted the behaviour demonstrated by the initiator); however, the social-learning process that was sufficient for the first half of the group to learn the target behaviour cannot be filtered out as an explanatory variable. More importantly, in this stage,

none of the subjects have adjusted their behaviour to the majority; they have 'merely' acquired the behaviour that gradually becomes the majority strategy. This means that in this diffusion process, the two main features of the conformity phenomenon are compromised: copying the majority and forgoing individually acquired behaviour. In this light, the pattern in which subjects revert back to the majority strategy after discovering an alternative may have more grounds to claim conformity (i.e. in this case it could be argued that an established behaviour needs to be discarded). However, in these reversion studies, where subjects re-converged on the majority strategy after exploring an alternative strategy, it remained unexplored whether the reverting individuals had had the chance to actually observe the majority and questionable to what extent reverting back to the first-learned strategy entails forgoing individually acquired behaviour (see van Leeuwen & Haun, 2013). Moreover, a recent study found that chimpanzees who perceived a majority of group members engaging in a different (yet equally effortful and rewarding) strategy from themselves did not adjust their behaviour to the majority (van Leeuwen et al., 2013). Contrary to the earlier mentioned conformity studies in chimpanzees (e.g. Hopper et al., 2011; Whiten et al., 2005), van Leeuwen et al. (2013) did not equate the majority strategy with the first-learned strategy of the minority chimpanzees, which enabled them to conclude that chimpanzees prefer their familiar strategy over conforming to the majority (see chapter 5). Another recent study, however, seems to demonstrate nicely that primates can both be adopting the majority strategy and forgoing their previously established behavioural preference, the two pillars of the conformity definition (van de Waal, Borgeaud & Whiten, 2013). In this study on wild vervet monkeys, *Chlorocebus aethiops*, both maturing and immigrating individuals adopted the foraging preference shared by the majority of the local group, indicating that at least the immigrants show conformity as it is defined in human psychology (van de Waal et al., 2013). However, the claim for selective majority copying remained circumstantial at most (authors' own conclusion, see supplementary materials in van de Waal et al., 2013). Indeed, the fact that most of the resident vervet monkeys used the foraging strategy to which the immigrants 'conformed' does not mean that the immigrants used this majority information in their foraging decisions. Recognizing that learning

entails a complex arena of individual, social and contextual characteristics (e.g. see Kendal, Coolen, & Laland, 2009), it might be that other learning biases have been at play during the acclimatization process of the immigrating males, such as a bias to value social information over individual information when the environment is uncertain (where a majority bias need not be at play).

The second issue that pertains directly to our focus of demarcating social from majority influences is related to the finding that chimpanzees who have acquired their behaviour socially have been shown to be relatively rigid in the use thereof, even at the cost of efficiency (Price, Lambeth, Schapiro, & Whiten, 2009). Importantly, Price et al. (2009) obtained these results in the scenario where the chimpanzees learned from one conspecific, not from a majority. A similar finding was reported by Whiten (1998): in this study, chimpanzees preferentially used their first-learned action pattern that had been demonstrated to them by one human experimenter, even after discovering that other sequences worked equally well (Whiten, 1998). These observations suggest that chimpanzees remain faithful to what they have learned first, or socially, and that these characteristics, not majority influences, can sufficiently account for the information diffusion and the reversion pattern that form the foundation of the conformity interpretation in primates (also see Hrubesch et al., 2009; Pesendorfer et al., 2009; van Leeuwen & Haun, 2013).

DO RATS SHOW CONFORMITY?

The conformity data in rats, *Rattus norvegicus*, are also a good example of the potent effects that social information can exert without it being transmitted by a majority of individuals. In an early conformity study, Konopasky & Telegdy (1977) showed that some rats would follow the unrewarded strategy option demonstrated to them by one 'leader' rat, even when they were experienced in choosing the rewarded option. More recent studies used a similar design in which 'observer' rats were shown to copy the foraging decision of one demonstrator rat, even when they had experienced those options to be unpalatable or even toxic (Galef & Whiskin, 2008; Jolles et al., 2011). In an attempt to shed light on the distinction between social and majority influences, Galef (2009) pointed to the findings in which naïve rats showed an increased

probability of adopting a demonstrated pattern of behaviour as the proportion of demonstrators increased (e.g. Chou & Richerson, 1992; Galef & Whiskin, 1995; see Galef, 2009). However, paraphrasing Galef's (2009) own conclusion, in the case of naïve individuals, the bias towards copying the majority can only be identified when the probability of adopting the majority strategy increases disproportionately compared with the increase in the relative majority size, which has not shown to be the case in any of the rat studies (Galef, 2009; Laland, 2004). In other words, the naïve rats may have responded to the amount of social information, regardless of it being transmitted by a majority of group members. More importantly for this review, however, is the fact that none of these latter studies investigated the tendency of knowledgeable rats to adopt social information, which invalidates an adequate comparison to the findings of the original human conformity studies.

DO FISH SHOW CONFORMITY?

Studies on conformity in fish have followed different approaches from experiments in other taxa and thus allow for slightly different interpretations. An early study by Day et al. (2001) showed that guppies, *Poecilia reticulata*, are hindered in their ability to locate food resources by the relative inertia of larger groups when visibility is compromised. The authors concluded that the guppies increasingly preferred to remain part of the group with increasing group size, and hence interpreted their findings in terms of 'positive frequency-dependent social learning, or conformity' (Day et al., 2001, p. 924; also see Lachlan, Crooks, & Laland, 1998; Laland & Williams, 1997 for similar findings and interpretations). This interpretation, however, has been criticized based on the consideration that guppies are a shoaling species and therefore let their behavioural choices become immersed in the collective group decision. In other words, as individual guppies by default prefer to swim in groups, their choices in such a group scenario, even if they were affected by majority influences, would be overshadowed by their shoaling preference (see Claidière & Whiten, 2012). Whether this critique is accepted or not, notwithstanding the interesting social effects revealed in this study, the fact that the guppies were not tested in a situation in which they needed to forgo their personal knowledge compromises a

valid comparison between the guppies' behaviour and the concept of conformity as originally defined in human psychology.

In an attempt to investigate this latter operationalization (conformity sensu Asch, 1956), researchers tested whether guppies would forgo their individually acquired information on food patch profitability under the influence of majority demonstrations. Although naïve subjects followed the majority convincingly, the knowledgeable subjects did not opt for exploring the food patch demonstrated by the majority, unless their individually acquired strategy was made relatively costly (Kendal et al., 2004). These findings indicate that guppies are susceptible to social information. However, owing to the conspicuous inequality in net strategy payoff (i.e. only the individually acquired strategy was made costly), they do not yet shed light on guppies' inclination to conform. In fact, the guppies could have chosen the majority option because it was energetically more efficient than their individually acquired strategy. Moreover, it remains to be investigated to what extent the guppies would have opted for the demonstrated food patch if there had been only one demonstrator (as in the rat studies).

More convincing evidence for conformity in fish comes from a study in sticklebacks. Pike and Laland (2010) showed that nine-spined sticklebacks, *Pungitius pungitius*, adjusted their food patch preference to the conflicting preference of the majority of demonstrators, contingent on the increasing (relative) majority size (Pike & Laland, 2010). In contrast to the studies in guppies, this stickleback study shows that fish may not just favour social information over individually acquired information, but may be specifically drawn to synchronizing their behaviour with the largest group of dissidents.

DO BIRDS SHOW CONFORMITY?

To our knowledge, claims of conformity in birds have not been made explicitly. However, several bird species have been shown to adjust their behaviour upon observing conspecifics demonstrating alternative preferences in a similar fashion to the rats in the aforementioned studies. For instance, indigo buntings, *Passerina cyanea*, were found to adjust features of their songs to the songs of nearby individuals (Payne, 1985) and zebra finches, *Taeniopygia*

guttata, adopted the foraging and mating preferences of conspecifics, even when this behaviour conflicted with their personal preferences (Rosa, Nguyen, & Dubois, 2012). Other studies implicitly corroborate these findings, for instance by showing that birds are likely to adopt local song dialects (e.g. Espmark, Lampe, & Bjerke, 1989; Mundinger, 1982) and breeding site preferences (e.g. Boulinier, McCoy, Yoccoz, Gasparini, & Tveraa, 2008; Brown, Bomberger Brown, & Danchin, 2000; Danchin, Boulinier, & Massot, 1998). However, although this kind of behavioural adjustment can lead to local behavioural convergence (i.e. a possible signature of conformity), the actual bias towards copying not just any demonstrated behaviour but the behaviour performed by the majority of group members remains to be demonstrated (e.g. see Haun, van Leeuwen, & Edelson, 2013).

DO INSECTS SHOW CONFORMITY?

The most relevant data from the insect literature for our discussion revolving around conformity comes from studies in which personal information was pitted against social information. For instance, it was recently shown that female fruit flies, *Drosophila melanogaster*, preferred to mate with poor-condition rather than good-condition males after observing the poor-condition but not good-condition males in close proximity with another female (i.e., indicating that those males were previously chosen by other females; Mery et al., 2009). Female fruit flies in control conditions (without any social information) showed a preference for good-condition males. In conjunction, these findings indicate that female fruit flies adjusted their mating behaviour to social information against personal preference. Another recent study showed that female fruit flies modified their oviposition preference after observing eight female conspecifics unanimously expressing interest in one particular (arbitrary) egg-laying medium (Battesti et al., 2012). Control conditions were used to establish that interaction with the demonstrators was necessary (and sufficient) to induce behavioural acquiescence in the observer flies, and as prior personal sampling had endowed the observers with the knowledge that both media were equally rewarding, these findings were interpreted as adjusting mating behaviour against personal preference.

Notwithstanding the value of these studies for our understanding of animals' individual and social information use, these results confirm the central argument of this review: social information can induce behavioural adjustment irrespective of majority influences. The fruit fly studies addressed above have impressively shown that social information can be a potent vector in the decision-making process of animals, even for those with 'miniature brains' (Leadbeater & Chittka, 2007b), but do not necessarily tie this social influence to a majority bias: whereas the first study only used single demonstrators (Mery et al., 2009), the latter did not quantify the impact of single or minority demonstrators, which would seem a necessary benchmark for interpreting the observed social influences in terms of majority influence (Battesti et al., 2012).

The insect literature alludes to at least two more intriguing avenues. First, the fruit fly studies point to the importance of operationalizing the 'distance' between subjects' original preference and the demonstrated alternative. For instance, the difference between poor- and good-condition males (see Mery et al., 2009) could plausibly be considered of a different order than the difference between a recently learned arbitrariness for egg-laying media and the demonstration of the usage of one particular medium by conspecifics (see Battesti et al., 2012). In the following sections, we propose that information on this distance measure, the extent to which subjects' pre-established behaviour deviates from the socially observed behaviour, is necessary for interpreting the magnitude of behavioural adjustments, including conformity. Second, researchers studying information use in bee species (e.g. *Apis mellifera* and *Bombus terrestris*) consistently approach decision making as an intricate process involving many related aspects, such as the cost of individual sampling, the success of individual information-gathering attempts and whether social information yields new or familiar knowledge (Biesmeijer & Seeley, 2005; Grüter, Leadbeater, & Ratnieks, 2010; Leadbeater & Chittka, 2005, 2007a). This approach is more in line with social influence theories (Latané & Wolf, 1981; Tanford & Penrod, 1984) than with the paradigmatic conformity interpretations where social influence is coarsely collapsed into 'the majority' (see Asch, 1956; Sherif, 1936). In the next sections, we address these two decision-making

approaches in more detail (i.e. conformity sensu Asch, 1956 and the social influence perspective sensu Latané & Wolf, 1981 and Tanford & Penrod, 1984).

HUMAN CONFORMITY REVISITED

Although the conformity phenomenon as a research topic stems from the realm of human social psychology, the evidence in favour of human conformity remains ambiguous. One aspect that may have contributed to this ambiguity concerns the details of the social-information source that induces conformity, where doubt has been cast on the claim that the feature ‘majority’ is pivotal to conformity (see Bond, 2005). Here, instead of presenting a general overview of the conformity findings in humans (reviewed in e.g. Bond, 2005; Haun et al., 2013; Morgan & Laland, 2012) and in order to facilitate valid cross-species comparisons, we scrutinize the paradigmatic human conformity studies in the same light of social and majority influences as the animal studies reviewed before.

In the seminal human psychology experiments conducted by Solomon Asch, in which subjects were asked to indicate which line (out of three) matched a given target-line in length, a consistent proportion of the adult subjects adjusted their individual opinion to the erroneous conviction of (at least) three confederates (see Asch, 1951, 1955, 1956). Asch consistently referred to this behavioural phenomenon in terms of majority influences (e.g. Asch, 1956), which as such was adopted by contemporary scientists (e.g. Allen, 1965; Cohen, Bornstein, & Sherman, 1973) and has remained a commonly used concept (e.g. see Bond, 2005). In line with the tenet of the current review, revisiting this behavioural phenomenon in light of the demarcation between social and majority influences brings up to two important aspects. First, it needs to be emphasized that in the Asch studies (Asch, 1951, 1955, 1956) the ‘distance’ between the subject’s original stance and the demonstrated alternative seems relatively large compared with most of the nonhuman conformity studies addressed here. Although this may seem trivial, it is our contention that the magnitude of conformity can only be adequately assessed when this distance is known or at least somehow operationalized (Starkweather, 1970; also see van Leeuwen & Haun, 2013). For instance, for each subject in the Asch studies, the

distance between his/her initial line judgement and the conflicting judgement of Asch's confederates (e.g. see Asch, 1956) might arguably be larger than the distance between the two equally effortful and productive token reward alternatives for each chimpanzee in the most cited chimpanzee conformity study (Whiten et al., 2005). Whereas the former distance exists between easily perceivable, factual stances (i.e. one line is objectively 'correct'), the latter distance is arbitrary with both options (individual versus majority) being equally likely to be 'correct' (i.e. there is no truth value inherent to the alternatives). This means that in these specific designs, it might take more social/majority influence to make the human subjects conform than it would take to make the chimpanzees conform. As such, this distance measure would be a valuable addition to the study of conformity (also see section 'Conclusion and future directions'). Moreover, identifying the inherent presence of this distance feature is useful for illustrating the meaning of the second aspect, which might be best described by the following question: 'do the subjects in the seminal social psychology studies conform because the alternative is demonstrated by the majority or do they give in to social influences (where again it should be noted that majority influences are inevitably social influences, whereas social influences do not have to be majority influences)?'. To answer this question, it may be essential to adopt the logical view that social information, just like individually acquired information, can have an intrinsic value apart from the value that subjects may attribute to 'the majority'. In other words, social information does not become informative and/or meaningful only when it is presented by a majority of group members; it has an impact on social animals regardless of this majority feature. Proponents of social-influence theories have adopted and found empirical support for this argument in humans (e.g. see Latané & Wolf, 1981; Tanford & Penrod, 1984). They have additionally posed that not the mere fact that individuals are confronted with a majority, but more nuanced parameters such as strength and immediacy of the social-influence sources and the number of demonstrators have an impact on the behavioural decision of the subjects. Similarly, animal studies have shown that species differ in their reliance on social information (Coolen, van Bergen, Day, & Laland, 2003; van Leeuwen, Call, & Haun, 2014) and that also other factors such as social-

rearing environment and experienced stress can affect animals' tendency to use social cues (guppies: Chapman, Ward, & Krause, 2008; Japanese quail, *Coturnix japonica*: Boogert, Zimmer, & Spencer, 2013). Taken together, these findings indicate that social influence is a vector of which the magnitude is determined by many more features than merely 'the majority'. In turn, this underlines the central claim of this review: differentiating between the effects of social and majority influences is necessary for validly interpreting 'conformity' findings and thus for providing a calibrated platform to compare conformity across species. For instance, the aforementioned studies in rats seem to indicate that subjects could adjust their previously learned (and even preferred) behaviour based on the information demonstrated by just one conspecific (Galef & Whiskin, 2008; Jolles et al., 2011). This finding shows that in a given species, social information can outweigh individual information irrespective of any majority bias. In turn, this finding implies the more general premise that in any species the values of social and individual information exist within an intricate trade-off that can, but does not necessarily have to, be moderated by the feature 'majority' (e.g. see Kendal et al., 2009; Kendal, Coolen, van Bergen, & Laland, 2005). In other words, if the value attributed to social information trumps the value attributed to individual information, then behaviour and/or convictions could be adjusted through the pull of social information without any majority influence. For instance, in the absence of any susceptibility to majority influences, animals could have evolved or learned preferences for social over individual information, or adjust their behaviour when social information provides a more recent sample of the environment than individual information.

Note that the distance feature and the possibility of having social but not majority influences at play are nicely reflected in the results from the Asch studies. Recapitulating, in these studies, subjects were asked to indicate which line (out of three) matched a given target-line in length (e.g. see Asch, 1956). The discrepancy between the subject's judgement and the intentionally erroneous judgement conveyed by Asch's confederate(s) might be considered large here because the task at stake is about an easily perceivable and straightforward factual quandary, i.e. subjects can be relatively sure of the correct answer. As such, the subjects may need more social weight in order to be swayed than one

confederate could provide. If this premise is accepted, additional social weight would be needed to make subjects adjust their opinion to the conflicting stance, which is consistent with the finding that at least three confederates unanimously need to express this conflicting position (e.g. Asch, 1956). Besides an illustration of how the distance measure could be tied to conformity, this also indicates that the increased social pressure could have been responsible for subjects' behavioural adjustment, not 'the majority' per se. Similarly, if the distance measure is meaningful, subjects should be more amenable to conform to the confederate(s) when the two conflicting stances differ less in their accuracy/profitability. This seems to be supported by the recent finding that 2-year-old children conform equally to one or three demonstrators when the two 'conflicting' strategies are equal on every level except for arbitrary location (i.e. which identically shaped pipe to drop a token into in order to receive a reward; Haun, Rekers & Tomasello, 2014).

The distinction between social and majority influences is further illustrated by some details of the original Asch studies: Whenever the focal subject finds himself not being the only dissenter from the majority conviction, conformity breaks down drastically, even when the other dissenter does not agree with the focal subject but instead indicates the third alternative judgment (Asch, 1956). Similar observations were made when the majority comprised only two confederates: the extent to which focal subjects conformed to the majority declined drastically in such scenarios (see Asch, 1951, 1955, 1956). Note that in both cases, the majority remained present, but was not conformed to. Minimally, these observations indicate that other features of social influences might have been at play and that the moderator of conformity 'to a majority' might be poorly grounded (see Mesoudi, 2009 for a more detailed analysis of the difficulty to attribute subjects' 'conformity' in the Asch studies to the majority).

Alluded to in previous sections, one stringent attempt has been made to pinpoint selective majority copying in the context of conformity research. This attempt stems from the cultural evolutionary framework, where the seminal work of Boyd and Richerson showed that in order to identify the bias to conform to the cultural variant that is used by the majority, one needs to show that the likelihood of copying the majority behaviour for a given individual increases

disproportionately compared with the increase of the relative majority size (Boyd & Richerson, 1985; Richerson & Boyd, 2005). For instance, when the relative majority size increases from 0.6 to 0.8 (proportion of the population), the likelihood with which a majority biased individual copies the majority would increase significantly more than 33.3%. The reasoning behind this criterion is that individuals who would copy the majority increasingly, but not to a disproportionate extent, could similarly copy any individual in the population randomly, thus without any selective majority considerations (see Henrich & Boyd, 1998; Mesoudi, 2009; van Leeuwen & Haun, 2013). One recent study on human adults' decision-making processes integrated this mathematical criterion into their analyses and found a substantial part of the subjects to be majority biased (Morgan, Rendell, Ehn, Hoppitt, & Laland, 2012). However, while this study impressively shows that humans rely on increasingly large majorities in the face of uncertain contingencies (which strategy leads to the highest rewards?), it only minimally tapped into subjects' inclination to forgo their prior behaviour as strategies were instantly chosen and the most rewarding strategy remained unknown until after the decision was made. This means that the individuals concerned did not have pre-established behavioural patterns that needed to be discarded; they rather assessed and reassessed their strategy upon each decision-making trial (in a way, this would be equal to a distance estimate being close to zero). In the current review we aim to clarify that the aspect of abandoning previously ingrained or preferred behaviour makes for a different information acquisition context from the cultural evolutionary definition of conformity in which naïve individuals are yet to establish their first behavioural pattern (i.e. when mathematically predicted to learn socially instead of individually, will majority considerations guide individuals' copying preferences?). One intuitive consideration that might clarify this difference pertains to the copying likelihoods: whereas the naïve individuals in the cultural evolutionary definition are already expected to copy behaviour from their group members, the very question of whether an individual adopts the presented social information forms the core of the human psychology definition. This means that where the naïve individuals already have a likelihood higher than 0.5 of ending up with the cultural variant of the majority based on 'random copying' (the

majority by definition comprises more than half of the individuals of the population), the knowledgeable individuals might be expected to stay true to their prior knowledge, especially in cases where the presented social information is conspicuously erroneous (as in the Asch studies, e.g. Asch 1956). Thus, adopting social information might reflect different underlying decision-making processes in these two scenarios (with the earlier discussed distance measure as a moderating variable for the magnitude of the decision-making process in the human psychology, but not the cultural evolutionary context of conformity). A related difference between the cultural evolutionary and human psychology approach to conformity pertains to their level of analysis: Where the former operationalization focuses on transmission biases and their population-level ramifications (e.g. conformist transmission leading to within-group homogeneity and between-group heterogeneity: Boyd & Richerson, 1985; Henrich & Boyd, 1998), the latter focuses on processes mediating behavioural responses on the individual level, which requires more specific psychological scrutiny (e.g. What is the value attributed to individual knowledge? What is the perceived efficacy of the socially demonstrated option?; see Kendal et al., 2009; Perreault, Moya, & Boyd, 2012; Rieucou & Giraldeau, 2011).

In sum, within the paradigmatic conformity operationalization in the study of human psychology, we have outlined similar difficulties in identifying the exact social source that is conformed to as in most animal studies. In the final section, we draw conclusions based on our review and delineate conceptual and empirical ways to demarcate social from majority influences and thus clarify the study of conformity.

CONCLUSION AND FUTURE DIRECTIONS

In this review, we have advocated the necessity of demarcating social influences from majority influences by showing that most of the animal conformity studies have confounded these related vectors. Whereas some conformity studies have not even incorporated a majority in their designs, others have not been able to control for social influences independent of the majority influence (cf. Pike & Laland, 2010). Even in the seminal human psychology studies (e.g. Asch, 1956), it remains unclear whether the subjects conformed

under mere social or actual majority influences. This begs the question of to what extent the ‘conformity interpretation’ in most of the studies reviewed here is justified and should be revisited in light of animals’ general susceptibility to social influences. The most important reason for doing so is empirical accuracy: only by identifying which social aspect feeds into the perception and subsequent behaviour of animals will we be able to discover which learning biases are pivotal in a species’ repertoire and compare these behavioural tendencies across species.

A theoretical and empirical distinction between social and majority influences is valuable, as it may prevent scholars from unwittingly interpreting social influences in terms of conformity (e.g. see van den Bos, Jolles, & Homberg, 2013). When scholars adhere to the cultural evolutionary definition of conformity, results should show that animals are disproportionately inclined to copy increasingly large relative majority sizes, while the aspect of ‘forgoing pre-established behaviour’ can accordingly be disregarded (but see Strimling, Enquist & Eriksson, 2009 for an important first approach to incorporating individuals’ reluctance to switch strategies into models of cultural evolution). However, when the human psychology definition of conformity is used, this very aspect of forgoing pre-established behaviour is central to the analysis and scholars should provide evidence that this pre-established behaviour is the subjects’ default strategy in the presence of alternatives but in the absence of conspecifics (thus forming one side of the distance measure; see previous section). To keep these two definitions apart, in earlier work, we have explicitly labelled the former definition ‘conformist transmission’ and the latter definition ‘conformity’, thereby using the labels coined in the respective research fields themselves (cultural evolution: e.g., Boyd & Richerson, 1985; Henrich & Boyd, 1998; human psychology: e.g., Asch, 1956; see Haun et al., 2013). Importantly, in both approaches to ‘conformity’, the distinction between social and majority influence is necessary for empirical accuracy. In the cultural evolutionary case, social influences are typically equated with ‘random copying’, which means that conspecifics are being imitated (i.e. evidence of social influence), but through an unbiased instead of a majority-biased strategy. This unbiased strategy yields behavioural convergence proportionate to the size of the majority (see previous

section), but fails to generate structural between-group variation: the very reason why scholars studying cultural evolution are interested in conformist transmission (e.g. see Boyd & Richerson, 1985). Thus, here, behavioural effects caused by social influences preclude interpretation in terms of 'conformist transmission' (e.g. see Laland, 2004; Richerson & Boyd, 2005). In the human psychology approach, forming the framework of this review, social influences may cause individuals to forgo their pre-established behaviour even when there is no majority present to conform to, which is clearly exemplified in the rat studies (Galef & Whiskin, 2008; Jolles et al., 2011). As such, the behavioural adjustments observed in rats after being exposed to one conspecific would not be considered conformity in the sense of the original operationalization (i.e. where the adjustment needs to be caused by the majority). In fact, this review has aimed to show that these social influences may have been underlying the purported conformity effects in many studies, even in the seminal human psychology ones.

The assumption that social instead of majority influences have affected observers, in some cases, seems to be straightforwardly confirmed by the fact that the conformity effect was already observed when the target individual was confronted with only one conflicting example (e.g. Galef & Whiskin, 2008; Haun et al., 2014; Jolles et al., 2011). Other cases remain inconclusive, as only a majority scenario was tested (e.g. Battesti et al., 2012; van de Waal et al., 2013; Whiten et al., 2005). What would have been observed if the subjects in these studies had been additionally tested in a single-model scenario? And if the subjects had adjusted their behaviour already in this single-model scenario, similar to the rats, what would have been the conclusion? In yet other cases, it became evident that the scope of social influences can stretch from the effect of one individual to the effect of many individuals before it turning into a majority influence (see previous section). For instance, three individuals may exert more social influence than one individual, but they still do not have to be the majority. In fact, it may be quintessential to acknowledge that these three individuals exert substantial social influence even when they are the majority (e.g. see Boyd & Richerson, 1985; Mesoudi, 2009). Furthermore, social influence can be more or less pressing depending on modifiers such as species, salience or perceived

efficacy (e.g. Latané & Wolf, 1981; Tanford & Penrod, 1984; also see Boogert et al., 2013; Chapman et al., 2008; Coolen et al., 2003; Kendal et al., 2009; van Bergen, Coolen & Laland, 2004). Thus, social influence is not a fixed effect, but a contingent vector with an associated magnitude. In more detail, the impact of social influence in any given situation is dependent on a plethora of ultimate and proximate determinants (e.g. species, life history, the characteristics of the model, previous social-learning experiences and the associated stakes of acquiring information; also see Laland, 2004; Kendal et al., 2009). To evidence conformity as the behavioural-adjustment effect caused by the majority, the effects of social influences need to be filtered out.

All the studies addressed in this review have provided valuable insights into the extent to which species incorporate socially demonstrated behaviour in their repertoires. The only proposition that we would like to advance based on the considerations related to social and majority influences, however, entails a more rigid specification of the social-learning features at play in any learning trade-off study. Especially in the case of conformity, we envision that definitional and empirical ambiguity could be reduced by elaborating on the exact source of behavioural adjustment. In principle, this could be done by describing the design details in relation to the specific social-learning bias under study. For instance, when studying conformity, efforts should be made to specify how the employed design differentiates between the majority bias, social influence (with its species- and context-dependent estimate) and biases pertaining to the characteristics of the individuals in the majority (e.g. kin, skill, prestige/dominance). Empirically, it could be a helpful heuristic to always design a conformity study such that the effects of both the majority and a single demonstrator are assessed. The results of such a comparison would already coarsely indicate whether a ‘group consideration’, a central feature of the conformity definition, is necessary to explain the results. In other words, if animals would already adjust their behaviour to match a single demonstrator, then clearly their acquiescence to a group of demonstrators (e.g. to a majority) could not be unequivocally interpreted in terms of conformity.

Additionally, we propose acknowledging the ‘distance’ between the pre-established behaviour of the focal subject and the behavioural alternative

presented by the majority as an important conformity variable. For instance, only by knowing parameters of the original stance of the focal subject (e.g. in terms of reinforcement history or relative preference) will its conformity become interpretable. One way to approach this aspect objectively might be to quantify the extent to which the focal subject persists in its stance in the presence of the alternatives, but in the absence of conspecifics. In the setting of the earlier mentioned line judgement task, during such a quantification, subjects will probably persist with high fidelity in choosing the correct line (see Corriveau & Harris, 2010). On the other hand, when confronted with two equally effortful and rewarding alternatives (e.g. the chimpanzees in Whiten et al., 2005), subjects may show a less pronounced (pre-established) preference for a given strategy. While such a setting-specific quantification may be an elaborate undertaking, it seems highly plausible that subjects' responses to social demonstrations are mediated by the magnitude of their initial preference.

Finally, we acknowledge that different motivations to conform have been identified. In their influential work, Deutsch & Gerard (1955) proposed using 'informational conformity' for cases where people conform because of their conviction that others comprise a trustworthy source of information about reality, and 'normative conformity' for cases where people conform in anticipation of inducing positive feelings in others (Deutsch & Gerard, 1955, also see Claidière & Whiten, 2012; van Schaik, 2012). As we aimed to focus specifically on clarifying the study of the social source to which subjects conform, we have not treated this motivational dimension in this review. However, this distinction between motivations is compatible with our proposed scrutiny. For instance, it could be found that subjects adjust their behaviour to 'one conspecific' for 'informational' reasons, or that subjects conform to 'a group of three strangers' for 'normative' reasons. Any combination of social source and motivation could in principle be possible, yet where the study of conformity motivations has been constructively delineated (Claidière & Whiten, 2012), with this review, we hope to have similarly advanced the need and structure for adequately identifying the social source responsible for individuals' behavioural adjustments.

Acknowledgements

This work was supported by the Comparative Cognitive Anthropology research group of the Max Planck Institute for Psycholinguistics. The authors are grateful to Katherine Cronin, Alex Mesoudi and three anonymous reviewers for helpful comments on an earlier version of the manuscript.

Human children rely more on social information than chimpanzees do

Chapter 7

Based on:

Van Leeuwen, E. J. C. & Haun, D. B. M. (2014). Human children rely more on social information than chimpanzees do. *Biology Letters*, 10, 20140487.

Abstract

Human societies are characterized by more cultural proliferation than chimpanzee communities. However, it is currently unclear what mechanism might be driving this difference. Since reliance on social information is a pivotal characteristic of culture, we investigated individual and social information reliance in children and chimpanzees. We repeatedly presented subjects with a reward-retrieval task on which they had collected conflicting individual and social information of equal accuracy in counterbalanced order. While both species relied mostly on their individual information, children but not chimpanzees searched for the reward at the socially demonstrated location more than at a random location. Moreover, only children used social information adaptively when individual knowledge on the location of the reward had not yet been obtained. These results support the interpretation that a heightened tendency to absorb social information may help explain why humans are more culturally diversified than chimpanzees.

Introduction

Culture, pivotally defined by socially transmitted information, is a more pronounced characteristic of human societies than of the societies of our closest living relatives (Richerson and Boyd 2005). Even in the most studied of our extant relatives, the chimpanzee, although culture has been identified (e.g., Luncz et al., 2012; van Leeuwen et al., 2012), its magnitude does not compare to the cultural richness of the human species (Mesoudi, 2011; Whiten & van Schaik, 2007). The reason for this cultural gap has been speculated upon. For instance, scholars have emphasized chimpanzees' conservative nature (e.g., Hrubesch et al., 2009; Marshall-Pescini & Whiten, 2008) and conjectured this predisposition to be impeding their cultural diversification (see Mesoudi 2011). However, direct comparisons to human's conservative tendencies have remained scarce and where the two species have been compared, chimpanzees did not prove to be more conservative than humans (Dean et al., 2012; also see van Leeuwen et al., 2013; Yamamoto et al., 2013). Others have asserted that humans, but not chimpanzees, are able to imitate each other and that this capacity may be the driving force behind human's relatively vast cultural proliferation (Galef, 1992; Tomasello, 1999; also see Hill, 2010; Tennie et al., 2009). While this may be true, empirical and theoretical work indicates that some forms of culture could also thrive without imitation (Caldwell & Millen, 2009; Heyes, 1993; Whiten et al., 2003). Hence these explanations alone provide insufficient accounts of the cultural gap (Mesoudi, 2011). A previously unconsidered explanation might be that humans place more value on social information than chimpanzees do and thus integrate more observed behaviours in their repertoires, which is the hallmark of cultural transmission (Richerson and Boyd 2005).

Therefore, we investigated whether children and chimpanzees place different value on social information. We explored this question with a simple reward-retrieval task in order to mimic natural contexts and boost subjects' motivation. Moreover, we tested subjects' social information reliance both in the presence and absence of equally informative individual information, thereby allowing for investigation of information reliance in two different contexts. With regard to the intrinsic information preferences of humans and chimpanzees, we predicted that both species prefer individual over social information because

individual information is more accurate across a broad range of conditions (Boyd & Richerson, 1985). In light of the documented cultural gap (Mesoudi, 2011), however, we additionally predicted that humans put more weight on social information than chimpanzees.

Methods

Ethics Statement

This study was approved by the Max Planck Institute for Psycholinguistics (Nijmegen) and Evolutionary Anthropology (Leipzig). With respect to the children: Signed informed-consent forms explaining the objective of the study and requesting for permission to conduct the study with the respective children had been obtained from the children's parents prior to the onset of the study. Children participated at their own kindergarten and were told that they could stop with the study anytime they wanted. With respect to the chimpanzees: We certify that we followed the "Principles for the Ethical treatment of nonhuman primates" (IPS & Society, 2007), that the research adhered to the ASAB/ABS Guidelines for the Use of Animals in Research, that all animal husbandry procedures were non-invasive and that participation by the animals was voluntary. Furthermore, the chimpanzees have access to an indoor (430 m²) and outdoor enclosure (4,000 m²). All enclosures include climbing structures, natural vegetation, and forms of enrichment (puzzle-boxes, jute bags, provisioning of concealed food). Normal diets were not restricted in this study; the chimpanzees gained extra food by participating.

Subjects and Procedure

We tested 23 German pre-school children (11 boys, 12 girls; $M_{\text{age}} = 3.7$ years, range = 3.0 - 4.6 years) at their Kindergartens and 14 chimpanzees at the Wolfgang Kohler Primate Research Center in Leipzig, Germany (5 males, 9 females; $M_{\text{age}} = 22.1$ years, range = 7.0 - 36.3 years). Subjects were presented with a task in which they had to select the correct location out of three options in order to obtain a reward (which was hidden under one of the three respective covers). Prior to this task (i.e., the *test* phase), the subjects had obtained

conflicting information regarding the correct location in the *acquisition* phase through individual exploration and demonstrations by a conspecific (Figure 1).

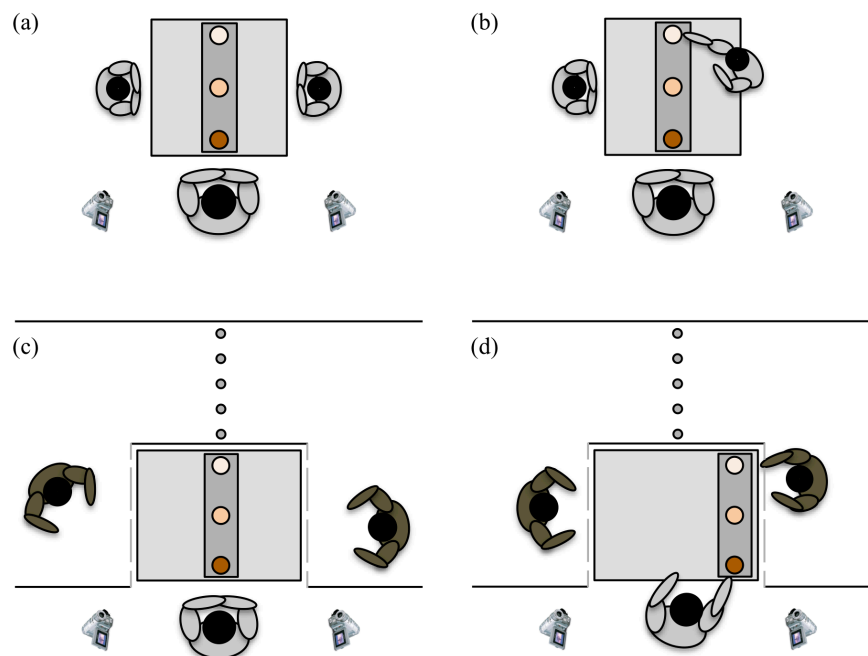


Figure 1. (a) Two children were seated at a table such that they faced each other. Three covers were placed in the middle of the table, in between the children. After giving a concise instruction, the Experimenter (at the head of the table) placed an occluder over the covers, showed the toy to both children and baited one of the covers with this toy. Subsequently, (b) one child was given its turn to choose one cover to explore, the other child observed this choice and its result. (c) Two chimpanzees were placed in adjacent rooms such that they could see each other, but not enter each other's room. Each chimpanzee had access to a choice window, which was a see-through perspex panel with three choice holes in them (left, middle, right; grey vertical bars in front of the chimpanzees). The two choice-windows were connected by a plastic tray (largest grey rectangle) on top of which another tray was placed that contained the three covers (small dark grey rectangle with three circles on top). After showing the grape to both individuals, E placed an occluder over the covers and baited one of them. Subsequently, (d) the small tray was slid towards one chimpanzee (in this case towards the chimpanzee on the right) who then indicated which cover it wanted to explore by putting one or several fingers through one of the choice holes. The chimpanzee was allowed to explore the cover by him/herself; after the cover was removed by the chimpanzee, E would lift up the cover entirely to make the choice and result also visible for the observing chimpanzee (in this case for the chimpanzee on the left).

For instance, in the *acquisition* phase, if a subject learned individually that the correct location was location A, this subject would learn *socially* that the correct location was B (or C). Subsequently, in the *test* phase, subjects would be tested for their inclination to search for the reward either at the location that

was baited during individual exploration, or the location that was observed to be baited throughout the social learning experience.

The *acquisition* phase, hence, comprised individual exploration and social learning. Individual exploration consisted of 10 successful trials (mean number of unsuccessful trials = 1.85). Success was defined as localizing the baited reward (only one attempt given). Social learning consisted of demonstrations given by a conspecific stooge and similarly comprised 10 successful trials (mean number of unsuccessful trials = 1.28) to balance individual and social learning in terms of informational value. A total of 23 different stooges were used for the children (all class-mates) and 14 different demonstrators (all group-mates) for the chimpanzees. Due to ethical and practical restrictions, male chimpanzees were mostly tested with female demonstrators (80%), whereas female chimpanzees were equally frequently tested with male and female demonstrators. Children were consistently tested with same-sexed stooges. In the absence of evidence for strong sex-biased copying heuristics in children and chimpanzees, to our best knowledge, we anticipate these slight methodological differences not to be significant for interpreting our results. Notably, theory would predict social learning in ‘uncertain’ contexts (Laland, 2004) – in this study the context where no individual information had been obtained yet – in principle regardless of further characteristics of the model, especially when only one model is present (i.e., where no preferential copying of one model over another is possible). The *test* phase comprised 10 trials per individual per condition, where each of the three covers were baited. Subjects were tested on their location preference individually to prevent further information acquisition by observation or any kind of audience effect from influencing the results.

All subjects participated in two independent conditions, which each comprised a separate information-acquisition phase (both individual and social learning) and a test phase (final preference testing). In one condition, subjects’ information reliance was assessed in a test phase following the acquisition phase after 2 minutes. In the other condition, the delay between the acquisition and test phase was set to 24 hours. To control for the order by which information was obtained, information acquisition was counterbalanced across and within

subjects (for an overview, see Table 1). Thus, this study comprised a between-subjects (within conditions) and within-subjects part (across conditions).

Table 1. Schema of experimental procedure. All subjects were tested twice; test 1 always preceded test 2. Information acquisition (individually and socially) was counterbalanced in order, both within and across conditions (test at 2-min or 24hrs). Test 1 and test 2 were carried out with different sets of covers as to minimize carry-over effects due to cover preferences.

<i>Procedure test 1</i>	<i>Procedure test 2</i>	<i>Children (n)</i>	<i>Chimpanzees (n)</i>
1. Individual information	1. Social information		
2. Social information	2. Individual information	6	4
3. Preference test after 2min	3. Preference test after 24hrs		
1. Social information	1. Individual information		
2. Individual information	2. Social information	5*	3
3. Preference test after 2min	3. Preference test after 24hrs		
1. Individual information	1. Social information		
2. Social information	2. Individual information	6	4
3. Preference test after 24hrs	3. Preference test after 2min		
1. Social information	1. Individual information		
2. Individual information	2. Social information	6	3
3. Preference test after 24hrs	3. Preference test after 2min		

*One drop-out because of random stooge behaviour

Analysis

Primarily, individuals' *first* location-choices in the test phases were analysed to preclude the influence of positive reinforcement across trials. We ran a Generalized Linear Mixed Model (GLMM; Baayen, 2008) with binomial error structure and logit link function. The predictor variables comprised species and condition (focal variables), order and sex (control variables), and subject (random effect). The response variable was initially set to "yes/no" reliance on *individually-acquired* information because preferential reliance on individual information is predicted as default strategy by the literature (e.g., Boyd & Richerson, 1985; Kendal et al., 2005). Additionally, we modelled subjects' reliance on *socially-acquired* information (same binomial error structure).

To enable inspection of means and errors, all 10 test trials were included in further analysis (both approaches yielded the same results). First inspection focused on subjects' information reliance after being exposed to both individual and social information (Figure 2a). Secondly, we investigated subjects' first location-choice after they had been exposed to social information only, in order to assess to what extent subjects would assimilate social information (Figure 2b).

Results

Information reliance after individual and social information acquisition

Across conditions, both children and chimpanzees relied significantly more on individually obtained information than on socially obtained information and the third (non-experienced) alternative combined (Intercept test, Wald estimate \pm SE = 1.16 ± 0.38 , $p = 0.002$ and 1.10 ± 0.46 , $p = 0.017$, respectively). The order of information acquisition and sex did not significantly affect the results (order: estimate \pm SE = 0.67 ± 0.59 , $p = 0.26$; sex: estimate \pm SE = -0.10 ± 0.62 , $p = 0.88$).

We detected a trend towards an interaction between the factors species and condition when modelling social information reliance (null-full model comparison: $\chi^2 = 6.88$, $df = 3$, $p = 0.076$; interaction test, model comparison: $\chi^2 = 4.70$, $df = 1$, $p = 0.029$). The order of information acquisition and sex did not significantly affect the results in this model either (order: estimate \pm SE = -0.97 ± 0.72 , $p = 0.18$; sex: estimate \pm SE = 0.86 ± 0.73 , $p = 0.24$).

Closer inspection of this interaction revealed that the chimpanzees progressed from minimal social information reliance in the 2-min condition (mean \pm SD = $5.0 \pm 16.1\%$) to a substantial reliance on social information in the 24-hrs condition (mean \pm SD = $28.6 \pm 36.8\%$). Notably, this increase in social information reliance was due to a choice pattern in the 24-hrs condition not being different from a random response (Pearson's Chi-squared test based on 2000 replicates: $\chi^2 = 2.00$, $p = 0.421$). The choice patterns of the chimpanzees in the 2-min condition ($\chi^2 = 10.97$, $p < 0.001$), and also the choice patterns of the children in the 2-min ($\chi^2 = 10.44$, $p < 0.01$) and 24-h condition ($\chi^2 = 8.01$, $p < 0.01$) were significantly different from a random response. The children maintained a rather equal social information reliance across the two conditions (mean \pm SD = $20.4 \pm 36.7\%$ and $17.0 \pm 33.4\%$; see Figure 2a).

Lastly, where the children significantly preferred social information over the third, non-experienced alternative in the 2-min condition (one-tailed Wilcoxon signed-rank test: $V = 45.5$, $p = 0.032$), the chimpanzees chose the random option more than the socially demonstrated one (see Figure 2a; *NS*).

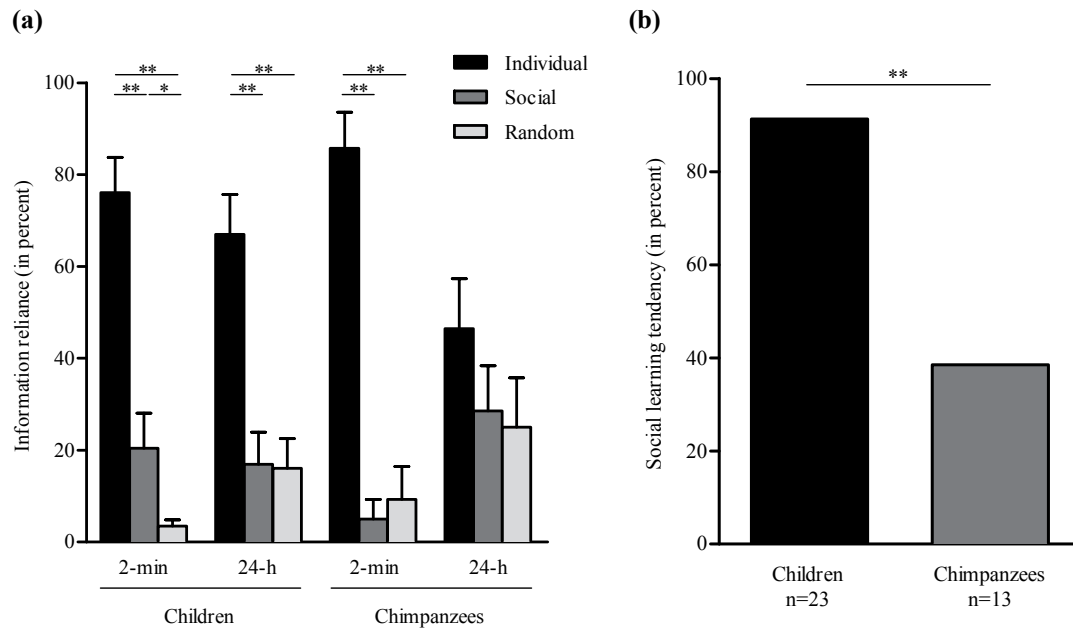


Figure 2. Children relied more on social information than chimpanzees. (a) Mean (+s.e.m.) information reliance for the children and chimpanzees across both time-delay conditions in per cent, and (b) per cent of children and chimpanzees who explored the location that had been observed to be rewarding for a conspecific during their first individual trial. One asterisk $p < 0.05$; two asterisks $p < 0.01$.

Social information reliance when only social information was obtained

Throughout the information acquisition phases, half the time social learning was followed by individual learning (see Table 1). Strikingly, where children used the social information in their first subsequent individual exploration (binomial test for probability being different from 0.33: 21/23 subjects, $p < 0.001$), chimpanzees did not (5/13 subjects, $p = 0.77$). Accordingly, children were more inclined to use social information than chimpanzees (Fisher exact test: $p < 0.002$, odds-ratio = 15.1; Figure 2b).

We ruled out the explanation that chimpanzees might have perceived the demonstrated location to be depleted by i) the general procedure making sure that the focal subject perceived that each trial one of the covers was rebaited – which was similar for children and chimpanzees – and ii) the observation that chimpanzees were not actively avoiding the location where the conspecific stooge had been successful (5 out of 13 chimpanzees used the social information to guide their first individual trial, which is an expected number based on a random choice-pattern (13 chimpanzees / 3 locations = 4.3 chimpanzees per

location) not on an actively avoidance-strategy. Moreover, after finding the correct location within their individual information acquisition phase, neither children (8/46 times) nor chimpanzees (5/28 times) deviated from that choice in subsequent trials, further indicating that subjects did not expect the chosen location to be depleted in the subsequent trial.

Importantly, while chimpanzees did not follow the socially demonstrated strategy on their first individual trial, they tended to be affected by the social demonstrations across all 10 individual trials (one-tailed Wilcoxon paired signed-rank test, social versus random choice: $V = 22.0$, $p = 0.080$). This result is consistent with the robust finding that chimpanzees are able to learn socially (e.g., Hopper et al., 2007; Whiten et al., 2007). The observation that chimpanzees nonetheless showed relatively little social learning tendencies compared to what could be expected based on previous research might be explained by the fact that the current task was relatively simple and did not require imitation of motor-pattern sequences (or *techniques*) in order to be solved (cf., Hopper et al., 2007; Whiten et al., 2007; also van Leeuwen et al., 2014). Chimpanzees might resort more to social learning when the behaviour at stake is difficult to acquire (e.g., nut-cracking: Luncz et al., 2012) and/or opaque in its workings (Horner & Whiten, 2005), while children may copy both easy (this study) and difficult actions more readily (e.g., Horner & Whiten, 2005; Lyons, Young & Keil, 2007).

Discussion

Children and chimpanzees relied more on their individual information than on equally accurate information presented to them by conspecifics, which is consistent with theoretical predictions on information usage in social animals. The children, however, searched for the reward at the socially demonstrated location more than at a random location (in the 2-min condition), while the chimpanzees never prioritized making use of their socially obtained information. Moreover, only the children used social information en masse to guide their subsequent individual exploration, which suggests that children considered social information more readily than chimpanzees.

Finding that children rely more on social information than chimpanzees may provide a novel addition to explanations for the cultural gap between

humans and chimpanzees (Mesoudi, 2011); i.e., humans' heightened inclination to assimilate observed behaviours could facilitate the emergence of within-group homogeneity, which is the hallmark of culture (Richerson and Boyd 2005). Note that the difference in social information reliance between children and chimpanzees was especially pronounced when subjects had not obtained individual information yet. Learning models predict that animals would incorporate social information when they are 'uncertain' (Laland, 2004), but based on our study, it could be hypothesized that where humans rely on their conspecifics, chimpanzees may prefer to diminish their uncertainty through additional individual exploration (also see Horner & Whiten, 2005).

The employed reward-retrieval task did not require sophisticated capacities to be solved; mechanisms like local- and stimulus enhancement could have allowed the subjects to learn socially. As such, the current comparison between children and chimpanzees seems to expose motivational rather than cognitive differences. Accordingly, in line with our postulated hypothesis and a recent study showing that chimpanzees 'recognize but fail to imitate successful actions' (Buttelmann et al., 2013), it might be that chimpanzees do not lack the capacity to understand the relevance of social information, but are less motivated to use it than humans (also see Over & Carpenter, 2011).

The fact that the children and chimpanzees were not of the same age might have contributed to the observed patterns. While testing juvenile chimpanzees and human adults seems like a necessary follow-up study, however, it is not implausible to assume that the observed responses reflect age-independent species differences. In most social learning studies in chimpanzees, adults have been tested and repeatedly found to learn socially adequately (e.g., Bonnie et al., 2007; Whiten et al., 2007; Hopper et al., 2007). Likewise, in humans, adults have been found to imitate even to a more irrational extent than children in so-called 'over-imitation' studies (McGuigan, Makinson & Whiten, 2011; Flynn & Smith, 2012). In conjunction, these findings indicate that the responses observed in the current study would also have been found when the test subjects would have been juvenile chimpanzees and human adults.

Another possible confound in the current study pertains to the reliability of individual and social information. The extent to which individuals have

perceived the individual and social information acquisition trials as reflecting reliable contingencies might depend on their unique set of previous experiences. Most notably, social learning experiences might be prone to yielding relatively ineffective information, e.g., when the ‘model’ performs an idiosyncratic or random act. For instance, models could put grass in their ears or explore multiple foraging options playfully, without the goal to effectively find food. Hence, the more pronounced reliance on social information by children compared to chimpanzees in the current study might be explained by the untested fact that the children have had substantially better experiences with social information than the tested chimpanzees. Although possible, we deem this explanation unlikely for the reason that the learning task in the current study consisted of a very simple and straightforwardly reinforced location puzzle.

Consistent with theoretical predictions (e.g., Richerson and Boyd 2005), we conclude that even culturally-rich species like humans and chimpanzees may prefer individual information over information obtained from conspecifics. The children’s responses parallel adults’ reliance on individual information in the presence of valuable social information across choice contexts (e.g., Efferson et al., 2008; Eriksson & Strimling 2009; Mesoudi 2011; Morgan et al., 2011), rather than children’s over-imitation tendencies reported in studies on imitation of motor patterns (e.g., Horner & Whiten 2005; Lyons, Young & Keil, 2007). Minimally, this finding highlights the fact that children do not favour social over individual information indiscriminately, which provides a new impetus for future research. Nevertheless, in the absence of individual information, children seem substantially more inclined to rely on social information than chimpanzees. Given that our study used a simple and ecologically relevant task in which humans’ and chimpanzees’ social information reliance were compared directly, our findings provide a novel and empirically grounded perspective on the striking difference between human and chimpanzee culture.

Acknowledgements

The authors are grateful to Sandy Kennert, Ronja Buechner and Felix Haiduk for collecting data at the Kindergartens and to the Leipzig Zoo chimpanzee keepers for their

invaluable assistance. We thank Katherine Cronin for helpful discussions, Roger Mundry for statistical advice and two anonymous reviewers for helpful comments on an earlier version of the manuscript. This research was funded by the Max Planck Institute.

Conclusions and General Discussion

Chapter 8

In this dissertation, I have investigated social learning dynamics of chimpanzees with the aim to better understand nonhuman primate behaviour and by extension human behaviour. On the one hand, acquiring knowledge about the specific ways in which other social animals organize their lives and how those strategies affect the interplay between (social) behaviour and (changing) environments teaches us about the many forms and functions of evolutionary processes. On the other hand, chimpanzees (together with the bonobos) are our closest living relatives and for that reason an interesting species to compare to humans (MacLean et al., 2012): By investigating social dynamics in closely related species, we may obtain valuable insights into our evolutionary blueprint.

In more detail, I have aimed to gain a more profound understanding of chimpanzees' cultural expressions, both in functional (what does this mean for the chimpanzees exactly) and comparative (how does chimpanzees' culture relate to human culture) terms. Following is a concise overview and discussion of the projects that I have worked on in light of these leitmotifs.

Summary

Can culture be identified in chimpanzees?

In order to find out whether chimpanzees have culture, behavioural differences between four chimpanzee communities were investigated and analysed in light of a stringent definition of culture (Perry et al., 2003; Whiten, 2003). In chapter 2, group-specific grooming tendencies within the so-called 'grooming hand-clasp' were central to analysis (McGrew & Tutin, 1978). This project was carried out in a Zambian sanctuary called 'Chimfunshi' where four stable groups of chimpanzees live under semi-captive conditions in one stretch of Miombo woodland. In summary, the grooming hand-clasp (GHC) is a specific grooming posture where two chimpanzees clasp onto each other's arms, raise

these arms up in the air, and groom each other with their other arm. The GHC is not part of the typical behavioural repertoire of chimpanzees and was therefore proposed to be a culturally transmitted trait (see McGrew & Tutin, 1978; Whiten et al., 1999). However, over time, the GHC has been observed in an increasing number of wild and captive populations and as such lost its initial appeal in light of nonhuman animal culture. My first project regains some of this initial appeal: chimpanzees use group-specific hand-clasp styles. These group specific styles were shared by all group members, stable over three points in time (2007, 2010, 2011) and not sufficiently explained by ecological, genetic or phenotypic determiners. In light of these new findings, we concluded that GHC behaviour is a socially transmitted trait with characteristics reminiscent of human culture (van Leeuwen et al., 2012).

In chapter 3, it was investigated whether chimpanzees are also inclined to copy arbitrary behaviour from their group members. Where the GHC behaviour entails an intense social interaction and most likely fulfils a function within chimpanzees' social dynamics (de Waal, 2001), the behaviour where chimpanzees put grass in their ears and leave it hanging there during subsequent activities seems less socially relevant and arguably without discernible function. Finding that chimpanzees copy this idiosyncratic behaviour would indicate that chimpanzees' social learning proclivities would allow for arbitrary fads which are central to human cultures (e.g., fashion trends). Similar to chapter 2, the focus of this study were the four groups of semi-captive chimpanzees at Chimfunshi. By analysing one year of systematically collected video material (\pm 720 hours), I found that 8 of the 12 chimpanzees belonging to the group of the grass-in-ear behaviour (GIEB) inventor engaged in GIEB, while only one GIEB occurrence was observed in one of the three other groups. The distribution of GIEB over all subjects was statistically unlikely to be due to chance. In conjunction with the fact that ecological and genetic influences are levelled out in the Chimfunshi set-up (the groups live in similar woodlands and are not sorted by subspecies), this result led us to conclude that chimpanzees spontaneously copy arbitrary behaviour, which again is reminiscent of human culture.

Are chimpanzees sensitive to majority influences?

As conforming to majorities has been identified as one of the main drivers behind cultural proliferation in humans (Richerson & Boyd, 2005), the next project examined whether majority influences would be similarly present in the social dynamics of chimpanzees. Thus, in chapter 4 and 5, it was investigated whether chimpanzees' cultural diversity may possibly come about through majority influences, of which conformity is one expression (see Haun et al., 2013). Chapter 4 entailed a critical review of the currently held conviction that conformity has been evidenced in chimpanzees (see Claidière & Whiten, 2012). After analysing methodological details, we advocated that the evidence in favour of conformity in chimpanzees thus far is not conclusive and that chimpanzees might have been acting out of a conservative nature instead (van Leeuwen & Haun, 2013; also see Hrubesch et al., 2009). Chapter 5 provided an empirical investigation of the theoretical critique advocated in chapter 4. Studying one group of chimpanzees in the Wolfgang Köhler Primate Research Center (Leipzig, Germany) and one group of chimpanzees in Chimfunshi, it became apparent that when conservatism and conformity are pitted against each other, chimpanzees act conservatively rather than conforming to the majority of group members. As a positive control and further empirical inquiry, conservatism was also pitted against the opportunity to obtain higher payoffs. In this scenario, chimpanzees abandoned their familiar strategy and adopted the more profitable one. Thus, we concluded that chimpanzees do not readily conform to majorities but do favour increased payoffs over their familiar strategy (van Leeuwen et al., 2013).

The relative value of social information

The social transmission of information is a pivotal feature of any definition of culture. For this transmission to occur, individuals need to recognize social information and integrate it into their own behaviour. My final project revolved around the relative value that animals attribute to social information, which was operationalized as the extent to which they adopt relevant social information both in the absence and presence of equally relevant individual information. First, however, an important distinction between social and majority influence was advanced. Chapter 6 entailed an extensive review of all

purported conformity findings across the nonhuman animal kingdom in light of this distinction. Following up on previous work (see chapter 4 and van Leeuwen & Haun, 2013), it was shown that many of the existing conformity findings can be alternatively understood in terms of animals' general susceptibility to social information. Most essentially, it became apparent that in most cases the effect of a single conspecific on the observer had not been taken as a benchmark for interpreting the majority effect. We concluded with suggestions to improve the study of animals' learning biases by using so-called 'differential diagnostics' procedures, by complementing majority influence manipulations with single-individual influence manipulations and by considering and quantifying the distance between the original behaviour of the focal individual and the behaviour expressed by the majority of group members. Subsequently, chapter 7 described the empirical investigation of information source preferences in chimpanzees and 3-4 year old children. An experimental procedure was developed in which chimpanzees and children obtained equally accurate individual and social information (social information was acquired from a conspecific model) about the location of a reward. The order by which the subjects obtained individual and social information was counterbalanced within and across subjects such that some subjects received individual information first and other subjects received social information first. The counterbalancing within subjects was done by including two test sessions: one after 2 minutes (following the last information acquisition session) and one after 24 hours. Results showed that both chimpanzees and children mostly relied on their individually acquired knowledge, regardless of the time delay between information acquisition and testing. However, in the trials where subjects received social information first, human children showed a stronger preference for integrating social information in their subsequent individual explorations than chimpanzees. We concluded that predictions on information usage when individuals are knowledgeable were confirmed (e.g., see Kendal et al., 2009), that children may be more poised toward using social information in the absence of individual information than chimpanzees, and that this latter finding may explain part of the difference in cultural proliferation between humans and chimpanzees (see Mesoudi, 2011).

General discussion

Group differences and the question of animal culture

We show that chimpanzees exhibit group differences in grooming hand-clasp preferences likely caused by social learning processes and that these differences are stable over time. One of the questions that remain is the proximate question of *how* (Tinbergen, 1963)? Through what mechanism(s) did the chimpanzees create and maintain their group-specific hand-clasp preference? We may conjecture that GHC behaviour was physically moulded in naïve chimpanzees by proficient claspers, rather than learned through mere observation (also see de Waal & Seres, 1997). One indication in favour of this conjecture is that mothers frequently engage in shaping their offspring's posture into a GHC posture (pers. obs.). By stretching one of their offspring's arms in the air and simultaneously grooming their offspring's exposed armpit, the mothers actively manoeuvre their offspring through the GHC routine. This way, the young generation obtains repeated proprioceptive exposure to the GHC behaviour, including the rewarding effect of the integral grooming part (see Photo 3).

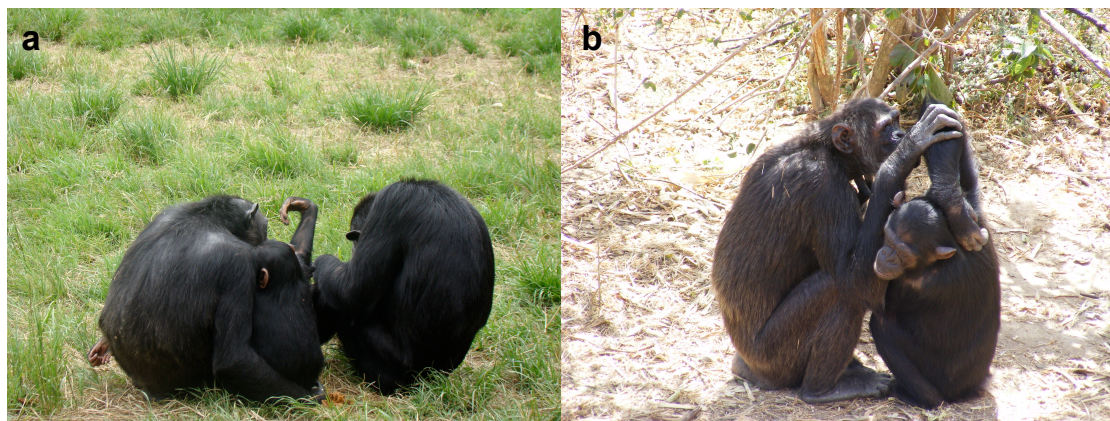


Photo 3. Mothers moulding the arms of youngsters into the typical handclasp postures; (a) Little Jane (left) holds the right arm of her daughter Little Jenkins by the elbow while grooming her upper arm; (b) Masya has lifted up Tilly's right arm in order to groom her elbow.

Thus, it is not inconceivable that young chimpanzees start exploring their GHC skills with other group mates after having experienced the behaviour frequently with their mothers and that they will go about the execution of the GHC behaviour in the same physically instructive way as their mothers started

off with. Interestingly, the Chimfunshi chimpanzees seem to additionally coordinate their GHC bouts in more subtle ways than mere physical action-and-acceptance sequences: Apparently contingent on relative (clasp-)familiarity, these chimpanzees seem to use gestures like the 'arm raise' and 'elbow tap' to indicate their readiness for a GHC interaction (Tacchetti et al., In preparation). Regardless of this possible gestural coordination aspect, however, the argumentation in favour of the moulding mechanism would be completed by some sort of founding effect: After initial invention of a particular style of hand-clasping, for instance the palm-to-palm style, the GHC behaviour could spread and become customary in the respective group with a group-specific style signature (which was evidenced in chapter 2).

Questions pertaining to this proximate level of explaining cultural group differences play a central role in the definitional quandary revolving around culture (e.g., see Galef, 1992; Hill, 2010). Some scholars have argued that culture should not merely be defined by stable between-group variation, but additionally by a cumulative quality, such that individuals obtain knowledge and skills that they would not have been able to invent by themselves in one life-time (Henrich & McElreath, 2003; Richerson & Boyd, 2005; Tennie et al., 2009). In light of this argument, it has been advocated that only the cognitively demanding mechanism 'imitation' could yield behavioural transmission of sufficiently high fidelity for such cumulative culture to take hold (e.g., Tomasello, 1999; Gergely & Csibra, 2005; Tennie et al., 2009; Hill, 2010). This is why scholars have focused on social learning mechanisms in nonhuman animals for decades (e.g., reviewed in Hoppitt & Laland, 2008; Galef, 2012; Nielsen et al., 2012) and why further empirical work on the proximate level might be a valuable future avenue for the GHC behaviour (and, by the same logic, for the GIEB, although imitation as underlying mechanism could already be inferred from the observations, see chapter 3). Taking up the gauntlet, however, imitation does not seem to be essential for culture to emerge. There seem to be many examples of cultural expressions in nonhuman animals that are likely not caused by forms of imitation (e.g., see Lefebvre, 1986; Byrne & Russon, 1998; Whiten et al., 1999; de Waal, 2001; Rendell & Whitehead, 2001; van Schaik et al., 2003; Grüter et al., 2010; van de Waal et al., 2013). Moreover, empirical and theoretical work shows

that culture can thrive in the absence of imitation (Heyes, 1993; Caldwell & Millen, 2009; Acerbi et al., 2012). Given these findings, even in light of the fact that imitation seems a capacity beyond the scope of most animal intelligence, animals would seem to be able to create cultural practices in much the same fashion as humans do (see chapter 7 for an appraisal of the *motivation* to incorporate social information as distinguishing humans and chimpanzees).

A peculiarity of the above discussions is that they revolve around differing opinions of what is referred to when one talks about ‘culture’. For instance, one could argue that animals are not cultural creatures because they do not imitate each other in the same way as humans do. On the other hand, one could argue that animals *do* engage in cultural practices because they show between-group variation not otherwise explained by genetics or ecology (see Alvard, 2003). Seemingly incompatible, these arguments are in principle not contradictory. For this reason, transcending the ‘cultural quandary’ beyond mere definitions seems a necessary step forward in terms of scientific clarity (also see Hill, 2010). If the locus of analysis were to be put central to the investigation instead of the *a priori* definition, then both principle and comparative explorations would be less prone to terminological ambiguity and thus empirical inaccuracy. In other words, turning back to the previously addressed arguments against and in favour of animal culture, the former would put ‘imitation’ central to their analysis whereas the latter would focus on socially learned group differences (as in this dissertation). Importantly, however, both accounts would refrain from additional interpretation in terms of ‘culture’. Unless both definitions of the entity under study (here: culture) are the same, there is no value in comparing the outcomes of different studies except for stressing their limitations.

With respect to our investigation of the GHC behaviour, therefore, it would be meaningful to follow up with studies exploring, for instance, the function of the behaviour, the mechanisms leading up to the observed style differences, and the question whether the next generations adopt the exact style preferences of the preceding generation, *in their own right*. Irrespective of the fact that some of these aspects may be part of some of the definitions that aim to capture the content of ‘culture’ (e.g., inter-generational transmission), we would focus on the value of these separate aspects for chimpanzees’ lives, such as the

surplus benefit of passing on locally-adaptive foraging techniques to their offspring, and permit ourselves comparative analyses (e.g., to humans) only on the level of similarly operationalized constructs.

Conformity in chimpanzees?

One of the concepts central to this dissertation is ‘conformity’: the tendency of observers to discard their personal behavioural in favour of the behaviour of the majority (Haun et al., 2013). Based on previous research, the conviction had emerged that chimpanzees show conformity in a similar fashion as humans do (Whiten et al., 2005; Hopper et al., 2011; see Claidière & Whiten, 2012; van den Bos et al., 2013). This conviction was based on the observation that chimpanzees remained faithful to the majority strategy, even in the presence of equally (Whiten et al., 2005) or more rewarding (Hopper et al., 2011) alternatives. Owing to methodological concerns, however, insights into chimpanzee conformity were precluded.

As elaborated on in chapter 4, in the concerning conformity studies, the chimpanzees’ first-learned and most familiar action patterns (with respect to the experimental task) equalled the action patterns displayed by the majority of group members. Thus, any attempt to interpret the behavioural patterns in light of majority influences falls short, for the chimpanzees could equally likely have been influenced by their reinforcement history with the respective alternatives, or, differently put, by their tendency to be conservative (also see Hrubesch et al., 2009; Pesendorfer et al., 2009). In light of this ambiguity, a new experimental design was developed in which chimpanzees’ alleged conformity could be disentangled from their conservative nature (see chapter 5). The respective study indicated that chimpanzees do not readily conform to majorities unless they can optimize their net revenue, and, perhaps more importantly, proposed a novel approach to the study of conformity through which our empirical discoveries can increase in accuracy and cross-species comparisons can be calibrated more validly.

This new approach to the study of chimpanzee conformity does not represent an exact match with the seminal human psychology studies (e.g., Asch, 1951, 1956). First and foremost, the human studies only found a significant

conformity effect when the dissenter was confronted with the majority in the absence of other dissenters. In other words, the minority consisted of one dissenter and, *ergo*, the majority was unanimous in its stance. The presented chimpanzee study (see chapter 5) differed from this format by having two and three individuals in the minority in study 1a and 1b, respectively. Second, the target individuals in the Asch studies consistently expressed a deviant stance compared to the majority because the task tapped into a problem which could both be easily evaluated and objectively solved. In other words, the line-judgment tasks represented factual problems which could be solved by a simple lengths assessment. In contrast, our chimpanzee study used behavioural alternatives (to distinguish the minority from the majority strategy) of exact equal difficulty where no perceptual input other than the subjects' decisions (and associated changes in the environment) would indicate one alternative as 'better' or 'more true' than the other. Taken together, these differences between the seminal human psychology studies and our chimpanzee approach preclude direct comparisons between human and chimpanzee subjects in light of the one central concept of 'conformity'. Thus, it could be argued that we should have conducted our chimpanzee study in the exact same way as the human psychology operationalization. On the other hand, it could be argued that our design may have favoured conformity more substantially than the psychology studies for the reason that the chimpanzees would not have to have adopted an erroneous or perceptually incorrect behaviour in order to conform. Following this argument, if chimpanzees are inclined to conform, it would have been expected to guide their decisions in this maximally facilitating design (maximally in the sense that no obstacles would have hampered their drive to conform other than switching strategies). But then again, the fact that we tested two and three minority subjects at a time, instead of one dissenter like in the psychology studies, might have neutralized this facilitating feature such that conformity would have been difficult to find in our design after all. Obviously, these considerations are of a speculative nature and more empirical studies will be needed to quantify their weights in chimpanzees' decision-making tendencies. Yet the most persuasive reason for us to adopt the design we ended up using was to put the earlier chimpanzee findings into perspective and, more importantly,

investigate circumstances under which chimpanzees may stop employing their familiar behaviour and switch to a novel strategy. In itself, this latter aspect forms a sufficient justification for our design for the reason that not so much the direct comparison to human conformity was pivotal to our research, but an understanding of behavioural patterns in freely-interacting chimpanzees (similar to our focus in the study of GHC and GIEB patterns). Thus, since behavioural decisions of this type ('should I stay or should I go') may have direct consequences for survival (e.g., foraging strategies, protection against predation), in line with the previously explained philosophy, our focus on the relevance of the observed behavioural patterns to chimpanzees' lives yields empirical value irrespective of its potential to enable cross-species comparisons.

Inevitably, however, one important aspect that we have missed in our study on conformity in chimpanzees is their natural habitat, with all its intricate and powerful selection pressures impossible to replicate in captive settings. While this point concerns the value of captive research more broadly (e.g., see Reader & Biro, 2010), its ramifications permeate through to the interpretation of specific conformity findings. For instance, if conformity renders the informational and social benefits attributed to it (e.g., Boyd & Richerson, 1985; Haun & Over, 2013), it might be considerably more vital to wild (immigrant) chimpanzees than to their captive counterparts (also see Luncz et al., 2012). For the former but not the latter, both the ecological and social environment change, which may require substantial adaptive capacities in order to cope with successfully. For instance, new foraging sites would need to be localized, new interaction patterns would need to be learned. And while chimpanzees are renowned for their individual learning skills, these new information packages may well be beyond the scope of trial-and-error sequences. Or they may be too risky to even try (e.g., encountering chimpanzees from a neighbouring community during foraging efforts might lead to substantial physical trauma, or failure to comply to local customs regarding the form and sequence of subordinate-dominant interactions may lead to harassment or a lack of male protection against the hostile resident females). On the other hand, one could argue that tendencies to conform to majorities would be present in the behavioural patterns of captive chimpanzees nonetheless, for their presence in

social animals' repertoires is predicted to be an evolved social learning strategy rather than a learned one (e.g., see Aoki & Feldman, 2013). As such, the earlier mentioned analysis on the level of experimental design features remains significant as they might meaningfully affect chimpanzees' conformist propensities.

A final consideration regarding chimpanzees' conformist tendencies concerns a frequently encountered conflation of social learning and conformity; an ambiguity that may benefit from interactive discussions. Restricted to monologues, here, I attempt to provide a starting point for this discussion by succinctly presenting the challenge. Essentially, confusion arises when social learning is equated to conformity without differential diagnostics. Claims have been made that when animals converge on a certain behavioural strategy in the presence of equally effective alternatives, they have conformed to the majority (e.g., see Perry, 2009; Hopper et al., 2011; Luncz & Boesch, 2014). Without the necessity to go into the study details, the fact that idiosyncratic behavioural strategies did not need to be discarded in favour of the majority strategy already puts the interpretation on the wrong track. More importantly, though, the fact that social learning in the absence of any bias has a high likelihood of leading to behavioural convergence renders interpretations in terms of conformity premature and therefore unsubstantiated. Besides, in some cases, the behavioural alternatives had not even been experienced by the target individuals, which not only precludes the possibility that the animals had forgone their strategies in favour of the majority, but also the reasoning that the individuals had actively *opted* to conform. It is with respect to this latter concern that scholars have distinguished between a mechanism-neutral conformity process, where the *behavioural outcome* of discarding behaviour in favour of the majority forms the central definition, and a specific majority bias, where behavioural convergence emerges through animals' *selective copying* of the majority (Haun et al., 2013; van Leeuwen & Haun, 2013). The former concern is pivotal to the convolution of social learning and conformity, however, and the fact that this concern pertains to a difference between behavioural plasticity and straightforward social learning processes should justify a closer inspection of the respective phenomena.

Social information preferences of chimpanzees and children

I have progressed from describing and discussing mere observations on cultural group differences in chimpanzees (GHC and GIEB) to exploring and testing the scope and existence of conformity in their behavioural repertoires. Partly, the reason for having done so is that conformity is a process and/or mechanism that could underlie the emergence and perpetuation of these group differences (e.g., see Henrich & Boyd, 1998; Richerson & Boyd, 2005). Finding that chimpanzees do not readily conform, however, indicates that perhaps other processes or mechanisms are responsible for the observed group differences. As we have seen in the previous section, mere social learning could also lead to behavioural convergence, thus in the absence of any majority influences. For this possibility to be real, chimpanzees need to be poised toward incorporating social information into their repertoires at least some of the time. While strong evidence exists that this premise is true (e.g., Bonnie et al., 2007; Whiten et al., 2007; Gruber et al., 2009), not much is known about chimpanzees' evaluation of social information when they already have relevant personal experience – a situation conceivably more accurate than its negation. In the following section of the discussion, findings are addressed that shed light on this empirical void.

Recapitulating, in a simple reward-retrieval task in which individuals were confronted with conflicting individual and social information, both chimpanzees and children relied mostly on their individually obtained solution. However, where children preferred social information over choosing a third, non-experienced option, the chimpanzees only seemed to converge on social information by chance (thereby potentially clouding an overall species difference). Moreover, during the task, children copied the choices of their conspecific models much more readily than chimpanzees did (chapter 7). Now while the former species-difference is hard to interpret, and would need replication with more fine-grained measures to distinguish between preference and random choice, the finding that chimpanzees relatively disregarded social information throughout the problem-solving phases was more robust and clear-cut. Although comparative research has its pitfalls (i.e., features and commodities could have different meanings for different species, e.g., see Maestriperi, 2012), the simple test set-up and the confirmation that both children and chimpanzees

were motivated and attentive throughout the experiments allow for the provisional conclusion that chimpanzees place less intrinsic value on social information than humans do. By ‘intrinsic’, here, I mean to refer to the quality of the entity itself (in this case the information units resulting from either individual or social learning endeavours), devoid of modifying factors like environmental predictability, associated reliability and acquisition costs. Thus, this study has yielded a first estimation of chimpanzees’ and children’s default information-preferences needed in order to interpret their decisions in contexts where information-reliance determinants are investigated. In a sense, this argument is reminiscent of the ‘distance’ concept advocated in chapter 6: Only by knowing the baseline parameter (or, the initial stance of the individual before being confronted with the deviating majority) will the final decision in the face of influential factors obtain sufficient reference for valid interpretation in terms of preferential information-reliance (or, in terms of the magnitude of conformity). Another parallel to the theoretical account in chapter 6 relates to the intrinsic value of social information. In chapter 6, I advocated the view that social information, like individual information, inevitably has a magnitude of significance for the individual perceiving and/or possessing it. In other words, the value of social information is not a fixed but a variable metric, depending on properties like idiosyncratic preferences, the content of the information and the extent to which it is ubiquitous. Moreover, and directly relevant for this discussion, species differences may exist with respect to this information source preference. For instance, where rats have been found to adopt social information readily (i.e., provided only briefly by one conspecific) and against their prior preference (Galef & Whiskin, 2008), chimpanzees have shown to be quite resistant to social influences, even when exerted continually by many of their group members (van Leeuwen et al., 2013). In our case, species differences in information reliance have thus been found between chimpanzees and humans, in a substantially controlled setting (see chapter 7). These findings have been related to the observation that humans engage in much more cultural practices than chimpanzees, which I view as a *consequence* of social learning rather than a qualitative difference in learning capacities or a *goal* in itself. But if this cultural watershed between humans and chimpanzees is caused by a more pronounced

tendency of humans to adopt social information, then why has this differential information-preference emerged (i.e., how did it come about, *sensu* Tinbergen, 1963)?

One simple yet intriguing explanation for the observed species-difference in chapter 7 could be related to population size and social organization. Human societies may have afforded more social information than chimpanzee societies because of their larger sizes and intricate social structure. By being exposed to social information more extensively, humans may have developed a more pronounced consideration of their social environment than chimpanzees (see Hill, 2010; Kobayashi & Ohtsuki, 2014 for similar conjectures). This reasoning was also advocated for explaining the technological divide between humans and the other extant ape species (Pradhan et al., 2012), and seems to be consistent with the recent finding that culture thrives better, i.e., more successful in inventing and maintaining adaptive solutions, with increasing population size (Derex et al., 2013; Richerson, 2013; Muthukrishna et al., 2014). In line with the findings presented in chapter 7, moreover, in the absence of any individual information, humans seem to increase their decision-making accuracy by relying on the wisdom of increasingly large crowds, which provides an *adaptive explanation* for increased social learning in dense social environments accordingly (King & Cowlishaw, 2007; Wolf et al., 2013). Hence, the children in our study (chapter 7) may have perceived their active conspecifics more as potential information producers than the chimpanzees did.

Taking a closer look, the emergent abundance of social information through socio-ecological shifts like the transition from nomadic to sedentary subsistence forms with rudimentary agriculture (see Bocquet-Appel, 2011) may have offered ideal circumstances for social information to be highlighted as a potentially rich source of valuable environmental feedback. If social learning consists of mechanisms and sequences that lie at the core of individual learning (which is currently under debate, e.g., see Behrens et al., 2008; Burke et al., 2010; Heyes, 2012), then, given that individual learning is an evolutionary old and widespread capacity and was most certainly among the capacities of early humans, all that may be needed to explain the evolution of increased reliance on social information is abundance (at least for some forms of social learning). In

other words, if information becomes increasingly available at no additional cost (i.e., no extra energetically costly perceptual instrumentation needs to evolve), then the value of that information will become more salient through mere exposure. In fact, rather than being a potentially costly activity, the sharing of information may well be regarded as one of the main benefits of group-living across animal taxa (van Schaik, 1983; CoussiKorbel & Frigaszy, 1995).

Obviously, however, the value of social information can only become salient when some form of evaluation process filters the observed acts according to pay-off. On the one hand, a simple associative system pivotal to individual learning capacities could fulfil this role (Galef, 1995). Without the necessity to experience the observed acts by themselves, individuals may be able to assess their efficacy using perceptual input only. On the other hand, repeated first-hand experiences with behavioural options of which their very possibility was offered by conspecifics (e.g., one innovative group member starts washing its food before eating it, or explores a new way of protection against predators) may generate positive reinforcement, which in turn could lead to biases for copying certain group members or even, given the 'right' circumstances, to preferential reliance on social information. Mathematical models have identified these 'right' circumstances under which social animals are expected to learn socially instead of individually (e.g., Henrich & Boyd, 1998; Kameda & Nakanishi, 2002; McElreath & Strimling, 2008; Aoki & Feldman, 2013). For instance, with increasing individual learning costs, modelled and real human individuals are more inclined to use social information (e.g., Kameda & Nakanishi, 2002; also see Laland, 2004). Similarly, when individuals encounter an environment with a markedly common cultural variant (as opposed to a close to equal prevalence of all existing variants), they are expected to adopt this most common variant with a higher than proportional likelihood, which is referred to as 'conformist transmission' (e.g., Henrich & Boyd, 1998; Nakahashi et al., 2012). Notably, as already addressed in chapter 1, social learning will not be wielded to obtain information when these 'right' circumstances are not met, i.e., when individual learning is superior in terms of adaptability (see Aoki & Feldman, 2013).

Although much work remains to be done to get a clear picture of the reality of the adaptiveness of these social learning strategies (see Galef, 2009),

some predicted patterns have been robustly observed in the empirical world (e.g., see Galef, 2006; Kendal et al., 2009). For instance, when individual knowledge becomes less reliable, animals seem to increasingly favour the adoption of social information (e.g., sticklebacks: van Bergen et al., 2004; bats: Jones et al., 2013). Similarly, when individual learning becomes increasingly risky, animals tend to rely more on social information (e.g., guppies: Kendal et al., 2004; rats: Galef & Yarkovsky, 2009). One of the most robust empirical confirmations of mathematical predictions pertains to animals' perception of environmental certainty. When animals are faced with relative environmental uncertainty, either through their naivety or through the fact that their individual information has become unreliable (Kendal et al., 2005), they seem to resort to social information (e.g., fowls: Nicol, 2004; guppies: Kendal et al., 2004; humans: Kameda & Nakanishi, 2002; Toelch et al., 2014; rats: Galef et al., 2008; also see Laland, 2004; Kendal et al., 2009). While this effect may in part be explained by the fact that social information is the only information that the animals have obtained and thus need not be specific to the *social* part of 'social information', it seems an effective way to increase the extent to which they can predict their environment and may as such be highly adaptive (consistent with the model predictions). Reiterating, this may also explain why almost all children in our study used the information produced by their partner throughout their information acquisition phases; they were still naïve to the contingencies of the experimental setting (chapter 7). In contrast, when the children had obtained both social and individual information, and thus lost their naivety or uncertainty, their situation may have been more comparable to the modelled scenario of 'non-selective' or 'unbiased' social learning in which individuals would either learn individually or adopt social information randomly. In this scenario, social animals are *not* predicted to rely on social information (reviewed in Aoki & Feldman, 2013). In conclusion, when individual information is available and there are no modifying factors that would favour social information beyond its intrinsic value (like risky or uncertain environments), relying on personal knowledge may be the most adaptive strategy.

Nevertheless, the human condition seems inextricably characterized by extensive social-information use, be it from the perspective of relative reliance

on social information under predicted circumstances, even in comparison to one of our closest living relatives known as a relatively cultural species (i.e., chimpanzees: e.g., see Whiten et al., 2003), or from the perspective that social learning may (have) become increasingly relevant in our rapidly expanding societies, with a recent study indicating that a nearly exclusive reliance on social learning outcompetes individual exploration even in many situations in which models would predict adaptive superiority of the latter strategy (Rendell et al., 2010). While the adaptive advantages of culture and its evolution toward increasingly complex configurations are evident (Alvard, 2003; Tennie et al., 2009), it will be intriguing and possibly unsettling to find out if culture will be smart enough to keep pace with the empirical world (Diamond, 2005).

Conclusions

My findings suggest that behavioural patterns of chimpanzees are not only instigated by genetic predispositions and idiosyncratic tendencies, but also by social learning processes leading to group-level traditions. These traditions may be formed around species-typical behaviour like social grooming (chapter 2), yet arbitrary, seemingly non-functional acts may also spread socially (chapter 3). Aiming at understanding the means by which chimpanzees converge on specific traditions, I conducted a methodological analysis (chapter 4) and empirically tested whether chimpanzees are susceptible to majority influences (chapter 5). Whereas chimpanzees proved capable of learning to switch their behavioural strategies for higher incentives, they did not adjust their behaviour to match the majority of group members, even though they observed themselves to be part of the minority. Elaborating on the possible role of conspecifics' behaviour in animal decisions, I subsequently proposed to demarcate social from majority influences in order to improve empirical accuracy (chapter 6). Where social and majority influences are confounded, I aimed to elucidate that social information is a vector with an associated estimate and that this estimate depends on individual, social and environmental factors, mediated by evolutionary selection pressures and/or learning experiences. Sparked by this principle, I compared the information preferences of children and chimpanzees and found that although both species predominantly relied on individual

information, children were markedly more inclined to use social information than chimpanzees, especially when tested in the absence of individual information c.q. uncertainty (chapter 7). While these findings provide valuable insights in species-typical information use, they may additionally help explain the pronounced difference in cultural proliferation between humans and chimpanzees, and shed light on which (social) factors may induce the motivation to learn from one's conspecifics.

References

- Acerbi, A., Jacquet, P. O. & Tennie, C. (2012). Behavioral constraints and the evolution of faithful social learning. *Current Zoology*, 58(2), 307-318.
- Allen, V. L. (1965). Situational Factors in Conformity. *Advances in Experimental Social Psychology*, 2(3), 133-175.
- Alvard, M. S. (2003). The adaptive nature of culture. *Evolutionary Anthropology*, 12, 136-149.
- Aoki, K. & Feldman, M. W. (2013). Evolution of learning strategies in temporally and spatially variable environments: A review of theory. *Theoretical Population Biology*, 90, 64-81.
- Asch, S. E. 1951 Effects of group pressure upon the modification and distortion of judgment. In *Groups, leadership and men* (ed. H. Guetzkow). Pittsburgh, PA, Carnegie Press.
- Asch, S. E. (1955). Opinions and social pressure. *Scientific American*, 193(5), 31-35.
- Asch, S. E. (1956). Studies of Independence and Conformity .1. A Minority of One against a Unanimous Majority. *Psychological Monographs*, 70(9), 1-70.
- Baayen, R. H. (2008). *Analyzing linguistic data*. Cambridge, UK: Cambridge University Press.
- Bandura, A. (1971). *Social Learning Theory*. New York: General Learning Press.
- Bates, D., Maechler, M. & Bolker, B. (2011). lme4: Linear mixed-effects models using S4 classes. R package version 0.999999-2. <http://CRAN.R-project.org/package=lme4>,
- Battesti, M., Moreno, C., Joly, D. & Mery, F. (2012). Spread of social information and dynamics of social transmission within *Drosophila* groups. *Current Biology*, 22, 309-313.
- Behrens, T. E. J., Hunt, L. T., Woolrich, M. W. & Rushworth, M. F. S. (2008). Associative learning of social value. *Nature*, 456(7219), 245-U45. Doi 10.1038/Nature07538
- Bergman, T. J. (2006). In response to: Social Cultures among Nonhuman Primates. *Current Anthropology*, 47(4), 648-649.

- Biesmeijer, J. C. & Seeley, T. D. (2005). The use of waggle dance information by honey bees throughout their foraging careers. *Behavioral Ecology and Sociobiology*, 59, 133-142.
- Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C. & Matsuzawa, T. (2003). Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. *Animal Cognition*, 6, 213-223.
- Bocquet-Appel, J.-P. (2011). When the world's population took off: the springboard of the neolithic demographic transition. *Science*, 333(6042), 560-561. Doi 10.1126/science.1208880
- Boesch, C. (2013). *Wild Cultures: A Comparison between Chimpanzee and Human Cultures*. Cambridge: CUP.
- Boesch, C. & Boesch, H. (1990). Tool use and tool making in wild chimpanzees. *Folia Primatologica*, 54, 86-99.
- Boesch, C., Head, J. & Robbins, M. M. (2009). Complex tool sets for honey extraction among chimpanzees in Loango National Park, Gabon. *Journal of Human Evolution*, 1-10.
- Bond, R. (2005). Group size and conformity. *Group Processes & Intergroup Relations*, 8(4), 331-354. Doi 10.1177/1368430205056464
- Bond, R. & Smith, P. B. (1996). Culture and conformity: A meta-analysis of studies using Asch's (1952b, 1956) Line judgment task. *Psychological Bulletin*, 119(1), 111-137.
- Bonnie, K. E. & de Waal, F. B. M. (2006). Affiliation promotes the transmission of a social custom: handclasp grooming among captive chimpanzees. *Primates*, 47(1), 27-34. Doi 10.1007/s10329-005-0141-0
- Bonnie, K. E., Horner, V., Whiten, A. & de Waal, F. B. M. (2007). Spread of arbitrary conventions among chimpanzees: a controlled experiment. *Proceedings of the Royal Society B-Biological Sciences*, 274(1608), 367-372. Doi 10.1098/rspb.2006.3733
- Bonnie, K. E. & de Waal, F. B. M. (2007). Copying without rewards: socially influenced foraging decisions among brown capuchin monkeys. *Animal Cognition*, 10, 283-292. Doi 10.1007/s10071-006-0069-9
- Bonnie, K. E., Milstein, M. S., Calcutt, S. E., Ross, S. R., Wagner, K. E. & Lonsdorf, E. V. (2012). Flexibility and Persistence of Chimpanzee (*Pan Troglodytes*) Foraging Behavior in a Captive Environment. *American Journal of Primatology*, 74(7), 661-668. Doi 10.1002/Ajp.22020

- Boogert, N. J., Zimmer, C. & Spencer, K. A. (2013). Pre- and post-natal stress have opposing effects on social information use. *Biology Letters*, 9. Doi 10.1098/rsbl.2012.1088
- Boulinier, T., McCoy, K. D., Yoccoz, N. G., Gasparini, J. & Tveraa, T. (2008). Public information affects breeding dispersal in a colonial bird: kittiwakes cue on neighbours. *Biology Letters*, 4, 538-540. Doi 10.1098/rsbl.2008.0291
- Boyd, R. & Richerson, P. (1985). *Culture and the Evolutionary Process*. Chicago: University of Chicago press.
- Boyd, R., Richerson, P. J. & Henrich, J. (2011). The cultural niche: Why social learning is essential for human adaptation. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 10918-10925. Doi 10.1073/Pnas.1100290108
- Boyd, R. & Richerson, P. J. (1995). Why does culture increase human adaptability? *Ethology and Sociobiology*, 16, 125-143.
- Brown, C. R., Bomberger Brown, M. & Danchin, E. (2000). Breeding habitat selection in cliff swallows: the effect of conspecific reproductive success on colony choice. *Journal of Animal Ecology*, 69, 133-142.
- Brown, R. L. (2013). Learning, evolvability and exploratory behaviour: extending the evolutionary reach of learning. *Biology & Philosophy*, 28, 933-955.
- Burke, C. J., Tobler, P. N., Baddeley, M. & Schultz, W. (2010). Neural mechanisms of observational learning. *Proceedings of the National Academy of Sciences of the United States of America*, 107(32), 14431-14436. Doi 10.1073/Pnas.1003111107
- Buttelmann, D., Carpenter, M., Call, J. & Tomasello, M. (2013). Chimpanzees, Pan troglodytes, recognize successful actions, but fail to imitate them. *Animal Behaviour*, 1-7. Doi 10.1016/j.anbehav.2013.07.015
- Byrne, R. W. & Russon, A. E. (1998). Learning by imitation: A hierarchical approach. *Behavioral and Brain Sciences*, 21(5), 667-721.
- Caldwell, C. A. (2009) Experimental Approaches to the Study of Culture in Primates. In L. S. Röska-Hardy and E. M. Neumann-Held (Eds.), *Learning from animals? Examining the nature of human uniqueness* (pp. 173-187). Hove: Psychology Press.
- Caldwell, C. A. & Millen, A. E. (2009). Social Learning Mechanisms and Cumulative Cultural Evolution: Is Imitation Necessary? *Psychological Science*, 20(12), 1478-1483.
- Cavalli-Sforza, L. L. & Feldman, M. W. (1981). *Cultural transmission and evolution: A quantitative approach*. Princeton, N.J.: Princeton University Press.

- Chapman, B. B., Ward, A. J. W. & Krause, J. (2008). Schooling and learning: early social environment predicts social learning ability in the guppy, *Poecilia reticulata*. *Animal Behaviour*, 76, 923-929. Doi 10.1016/j.anbehav.2008.03.022
- Chou, L. S. & Richerson, P. J. (1992). Multiple Models in Social Transmission of Food Selection by Norway Rats, *Rattus-Norvegicus*. *Animal Behaviour*, 44(2), 337-343.
- Claidière, N., Bowler, M. & Whiten, A. (2012). Evidence for Weak or Linear Conformity but Not for Hyper-Conformity in an Everyday Social Learning Context. *Plos One*, 7(2), e30970.
- Claidière, N. & Whiten, A. (2012). Integrating the Study of Conformity and Culture in Humans and Nonhuman Animals. *Psychological Bulletin*, 138(1), 126-145. Doi 10.1037/A0025868
- Cohen, J. (1960). A coefficient of agreement for nominal scales. *Educational and Psychological Measurement*, 20(1), 37-46.
- Cohen, R., Bornstein, R. & Sherman, R. C. (1973). Conformity Behavior of Children as a Function of Group Makeup and Task Ambiguity. *Developmental Psychology*, 9(1), 124-131. Doi 10.1037/H0035082
- Coolen, I., van Bergen, Y., Day, R. L. & Laland, K. (2003). Species difference in adaptive use of public information in sticklebacks. *Proceedings of the Royal Society B-Biological Sciences*, 270, 2413-2419. Doi 10.1098/rspb.2003.2525
- Corriveau, K. H., Fusaro, M. & Harris, P. L. (2009). Going With the Flow : Preschoolers Prefer Nondissenters as Informants. *Psychological Science*, 20(3), 372-377. Doi 10.1111/j.1467-9280.2009.02291
- Corriveau, K. H. & Harris, P. L. (2010). Preschoolers (Sometimes) Defer to the Majority in Making Simple Perceptual Judgments. *Developmental Psychology*, 46(2), 437-445. Doi 10.1037/a0017553
- Coultas, J. C. (2004). When in Rome... An evolutionary perspective on conformity. *Group Processes & Intergroup Relations*, 7(4), 317-331. Doi 10.1177/1368430204046141
- CoussiKorbel, S. & Frigaszy, D. M. (1995). On the relation between social dynamics and social learning. *Animal Behaviour*, 50, 1441-1453. Doi 10.1016/0003-3472(95)80001-8
- Cronin, K. A., Van Leeuwen, E. J. C., Vreeman, V. & Haun, D. B. M. (2014). Population-level variability in the social climates of four chimpanzee societies. *Evolution & Human Behavior*. Doi 10.1016/j.evolhumbehav.2014.05.004

- Danchin, E., Blanchet, S., Mery, F. & Wagner, R. H. (2010). Do invertebrates have culture? *Communicative & Integrative Biology*, 3(4), 303-305.
- Danchin, E., Boulinier, T. & Massot, M. (1998). Conspecific Reproductive Success and Breeding Habitat Selection: Implications for the Study of Coloniality. *Ecology*, 79, 2415-2428.
- Danchin, E., Charmantier, A., Champagne, F. A., Mesoudi, A., Pujol, B. & Blanchet, S. (2011). Beyond DNA: integrating inclusive inheritance into an extended theory of evolution. *Nature Reviews*, 12, 475-486.
- Darwin, C. R. (1859). *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. London: John Murray.
- Day, R. L., MacDonald, T., Brown, C., Laland, K. N. & Reader, S. M. (2001). Interactions between shoal size and conformity in guppy social foraging. *Animal Behaviour*, 62, 917-925.
- de Waal, F. (2001). *The ape and the sushi master: cultural reflections of a primatologist*. New York: Basic Books.
- de Waal, F. B. M. (1999). Cultural primatology comes of age. *Nature*, 399, 635-636.
- de Waal, F. B. M. (2010). *The Age of Empathy: Nature's Lessons for a Kinder Society*. New York: Three Rivers Press.
- de Waal, F. B. M. & Seres, M. (1997). Propagation of handclasp grooming among captive chimpanzees. *American Journal of Primatology*, 43, 399-346. Doi 10.1002/(SICI)1098- 2345(1997)43:4
- Dean, L. G., Kendal, R. L., Schapiro, S. J., Thierry, B. & Laland, K. N. (2012). Identification of the Social and Cognitive Processes Underlying Human Cumulative Culture. *Science*, 335(6072), 1114-1118. Doi 10.1126/Science.1213969
- Derex, M., Beugin, M-P., Godelle, B. & Raymond, M. (2013). Experimental evidence for the influence of group size on cultural complexity. *Nature*, 503, 389-391. Doi 10.1038/nature12774
- Deutsch, M. & Gerard, H. B. (1955). A study of normative and informational social influences upon individual judgment. *The Journal of Abnormal and Social Psychology*, 51(3), 629-636.
- Diamond, J. (2005). *Collapse: How societies choose to fail or survive*. London: Penguin Group.

- Dindo, M., Thierry, B. & Whiten, A. (2008). Social diffusion of novel foraging methods in brown capuchin monkeys (*Cebus apella*). *Proceedings of the Royal Society B-Biological Sciences*, 275(1631), 187-193. Doi 10.1098/rspb.2007.1318
- Dindo, M., Whiten, A. & de Waal, F. B. M. (2009). In-Group Conformity Sustains Different Foraging Traditions in Capuchin Monkeys (*Cebus apella*). *Plos One*, 4(11), e7858 10.1371/journal.pone.0007858
- Dukas, R. (2013). Effects of learning on evolution: robustness, innovation and speciation. *Animal Behaviour*, 85(5), 1023-1030. Doi 10.1016/j.anbehav.2012.12.030
- Efferson, C., Lalive, R., Richerson, P. J., McElreath, R. & Lubell, M. (2008). Conformists and mavericks: the empirics of frequency-dependent cultural transmission. *Evolution and Human Behavior*, 29(1), 56-64. Doi 10.1016/J.Evolhumbehav.2007.08.003
- Enquist, M., Eriksson, K. & Ghirlanda, S. (2007). Critical social learning: A solution to Rogers's paradox of nonadaptive culture. *American Anthropologist*, 109(4), 727-734. Doi 10.1525/Aa.2007.109.4.727
- Eriksson, K., Enquist, M. & Ghirlanda, S. (2007). Critical points in current theory of conformist social learning. *Journal of Evolutionary Psychology*, 5, 67-87. Doi 10.1556/JEP.2007.1009
- Eriksson, K. & Strimling, P. (2009). Biases for acquiring information Individually rather than socially. *Journal of Evolutionary Psychology*, 7(4), 1-21. Doi 10.1556/JEP.7.2009.4.4
- Espmark, Y. O., Lampe, H. M. & Bjerke, T. K. (1989). Song Conformity and Continuity in Song Dialects of Redwings *Turdus iliacus* and Some Ecological Correlates. *Ornis candinavica*, 20, 1-12.
- Fisher, R. A. (1930). *The Genetical Theory of Natural Selection*. Oxford: Clarendon Press.
- Fisher, R. A. (2003). *The Genetical Theory of Natural Selection: A complete variorum edition*. Oxford, NY: Oxford University Press.
- Flynn, E. & Smith, K. (2012). Investigating the mechanisms of cultural acquisition: How pervasive is overimitation in adults? *Social Psychology*, 43, 185-195. Doi : 10.1027/1864-9335/a000119
- Galef, B. G. (1992). The question of animal culture. *Human Nature*, 3, 157-178.
- Galef, B. G. (1995). Why Behavior Patterns That Animals Learn Socially Are Locally Adaptive. *Animal Behaviour*, 49(5), 1325-1334. Doi 10.1006/Anbe.1995.0164

- Galef, B. G. (2006) Theoretical and empirical approaches to understanding when animals use socially acquired information and from whom they acquire it. In J. R. Lucas and L. V. Simmons (Eds.), *Essays in Animal Behaviour: Celebrating 50 Years of Animal Behaviour* (pp. 161-182). San Diego: Academic Press.
- Galef, B. G. (2009). Strategies for Social Learning: Testing Predictions from Formal Theory. *Advances in the Study of Behavior, Vol 39*, 39, 117-151. Doi 10.1016/S0065-3454(09)39004-X
- Galef, B. G. (2012). Social learning and traditions in animals: evidence, definitions, and relationship to human culture. *Wiley Interdisciplinary Reviews-Cognitive Science*, 3(6), 581-592. Doi 10.1002/Wcs.1196
- Galef, B. G., Dudley, K. E. & Whiskin, E. E. (2008). Social learning of food preferences in 'dissatisfied' and 'uncertain' Norway rats. *Animal Behaviour*, 75, 631-637. Doi 10.1016/J.Anbehav.2007.06.024
- Galef, B. G. & Giraldeau, L. A. (2001). Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Animal Behaviour*, 61, 3-15.
- Galef, B. G. & Whiskin, E. E. (1995). Learning socially to eat more of one food than of another. *Journal of Comparative Psychology*, 109, 99-101.
- Galef, B. G. & Whiskin, E. E. (2008). 'Conformity' in Norway rats? *Animal Behaviour*, 75, 2035-2039. Doi 10.1016/J.Anbehav.2007.11.012
- Galef, B. G. & Yarkovsky, N. (2009). Further studies of reliance on socially acquired information when foraging in potentially risky situations. *Animal Behaviour*, 77, 1329-1335.
- Gergely, G. & Csibra, G. (2005). The social construction of the cultural mind: Imitative learning as a mechanism of human pedagogy. *Interaction Studies*, 6(3), 463-481.
- Goodall, J. (1968). The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Animal Behavior Monographs*, 1, 161-311.
- Goodall, J. (1986). *The chimpanzees of Gombe: patterns of behavior*. Boston: Harvard University Press.
- Gruber, T., Muller, M. N., Strimling, P., Wrangham, R. W. & Zuberbühler, K. (2009). Wild Chimpanzees Rely on Cultural Knowledge to Solve an Experimental Honey Acquisition Task. *Current Biology*, 19, 1806-1810.
- Grüter, C., Leadbeater, E. & Ratnieks, F. L. W. (2010). Social Learning: The Importance of Copying Others. *Current Biology*, 20, 683-685.

- Hanus, D. & Call, J. (2011). Chimpanzee problem-solving: contrasting the use of causal and arbitrary cues. *Animal Cognition*, 14(6), 871-878. Doi 10.1007/S10071-011-0421-6
- Hanus, D., Mendes, N., Tennie, C. & Call, J. (2011). Comparing the Performances of Apes (Gorilla gorilla, Pan troglodytes, Pongo pygmaeus) and Human Children (Homo sapiens) in the Floating Peanut Task. *Plos One*, 6(6). Doi 10.1371/journal.pone.0019555_ARTN e19555
- Hastie, R. & Kameda, T. (2005). The robust beauty of majority rules in group decisions. *Psychological Review*, 112(2), 494-508. Doi 10.1037/0033-295x.112.2.494
- Haun, D. B. M. & Over, H. (2013). A Homophily-Based Account of Human Culture. In P. J. Richerson and M. H. Christiansen (Eds.), *Cultural evolution: Society, Technology, Language, and Religion*. Cambridge, MA: MIT Press.
- Haun, D. B. M., Rekers, Y. & Tomasello, M. (2012). Majority-biased transmission in chimpanzees and human children, but not orangutans. *Current Biology*, 22, 727-731. Doi 10.1016/j.cub.2012.03.006
- Haun, D. B. M., Rekers, Y. & Tomasello, M. (2014). Great apes stick with what they know; children conform to others. *Psychological Science*
- Haun, D. B. M. & Tomasello, M. (2011). Conformity to Peer Pressure in Preschool Children. *Child Development*, 82(6), 1759-1767. Doi 10.1111/j.1467-8624.2011.01666.x
- Haun, D. B. M., van Leeuwen, E. J. C. & Edelson, M. G. (2013). Majority influence in children and other animals. *Developmental Cognitive Neuroscience*, 3, 61-71.
- Henrich, J. & Boyd, R. (1998). The evolution of conformist transmission and the emergence of between-group differences. *Evolution and Human Behavior*, 19(4), 215-241.
- Henrich, J. & McElreath, R. (2003). The evolution of cultural evolution. *Evolutionary Anthropology*, 12, 123-135. Doi 10.1002/evan.10110
- Heyes, C. (2012). What's Social About Social Learning? *Journal of Comparative Psychology*, 126(2), 193-202. Doi 10.1037/A0025180
- Heyes, C. M. (1993). Imitation, culture and cognition. *Animal Behaviour*, 46, 999-1010.
- Heyes, C. M. (1994). Social-Learning in Animals - Categories and Mechanisms. *Biological Reviews of the Cambridge Philosophical Society*, 69(2), 207-231. Doi 10.1111/J.1469-185x.1994.Tb01506.X

- Hill, K. (2010). Experimental studies of animal social learning in the wild: Trying to untangle the mystery of human culture. *Learning & Behavior*, 38(3), 319-328. Doi 10.3758/LB.38.3.319
- Hobaiter, C. & Byrne, R. W. (2010). Able-Bodied Wild Chimpanzees Imitate a Motor Procedure Used by a Disabled Individual to Overcome Handicap. *Plos One*, 5(8), ARTN e11959. Doi 10.1371/journal.pone.0011959
- Hopper, L. M., Schapiro, S. J., Lambeth, S. P. & Brosnan, S. F. (2011). Chimpanzees' socially maintained food preferences indicate both conservatism and conformity. *Animal Behaviour*, 81(6), 1195-1202. Doi 10.1016/j.anbehav.2011.03.002
- Hopper, L. M., Spiteri, A., Lambeth, S. P., Schapiro, S. J., Horner, V. & Whiten, A. (2007). Experimental studies of traditions and underlying transmission processes in chimpanzees. *Animal Behaviour*, 73, 1021-1032. Doi 10.1016/j.anbehav.2006.07.016
- Hoppitt, W. & Laland, K. N. (2008). Social processes influencing learning in animals: A review of the evidence. *Advances in the Study of Behavior*, Vol 38, 38, 105-165. Doi 10.1016/S0065-3454(08)00003-X
- Hoppitt, W. & Laland, K. N. (2013). *Social learning: An introduction to Mechanisms, Methods, and Models* Oxfordshire UK: Princeton University Press.
- Horner, V., Proctor, D., Bonnie, K. E., Whiten, A. & de Waal, F. B. M. (2010). Prestige Affects Cultural Learning in Chimpanzees. *Plos One*, 5(5), e10625. Doi 10.1371/journal.pone.0010625
- Horner, V. & Whiten, A. (2005). Causal knowledge and imitation/emulation switching in chimpanzees (Pan troglodytes) and children (Homo sapiens). *Animal Cognition*, 8, 164-181. Doi 10.1007/s10071-004-0239-6
- Horner, V., Whiten, A., Flynn, E. & de Waal, F. B. M. (2006). Faithful replication of foraging techniques along cultural transmission chains by chimpanzees and children. *Proceedings of the National Academy of Sciences of the United States of America*, 103(37), 13878-13883. Doi 10.1073/pnas.0606015103
- Hrubesch, C., Preuschoft, S. & van Schaik, C. (2009). Skill mastery inhibits adoption of observed alternative solutions among chimpanzees (Pan troglodytes). *Animal Cognition*, 12(2), 209-216. Doi 10.1007/s10071-008-0183-y
- Humle, T., Colin, C. & Raballand, E. (2009). Preliminary report on hand-clasp grooming in sanctuary-released chimpanzees, Haut Niger National Park, Guinea. *Pan Africa News*, 16(1), 7-10.

- Humle, T. & Matsuzawa, T. (2001). Behavioural Diversity among the Wild Chimpanzee Populations of Bossou and Neighbouring Areas, Guinea and Côte d'Ivoire, West Africa. *Folia Primatologica*, 72, 57-68.
- Humle, T., Snowdon, C. T. & Matsuzawa, T. (2009). Social influences on ant-dipping acquisition in the wild chimpanzees (*Pan troglodytes verus*) of Bossou, Guinea, West Africa. *Animal Cognition*, 12, S37-S48.
- IPS & Society, I. P. (2007). Principles for the Ethical Treatment of Non-Human Primates. http://www.internationalprimatologicalsociety.org/docs/IPS_ethical_guidelines_FINAL.pdf
- Jenness, A. (1932). The role of discussion in changing opinion regarding a matter of fact. *Journal of Abnormal Social Psychology*, 27, 279-296. Doi 10.1037/h0074620
- Jolles, J. W., de Visser, L. & van den Bos, R. (2011). Male Wistar rats show individual differences in an animal model of conformity. *Animal Cognition*, 14(5), 769-773. Doi 10.1007/S10071-011-0395-4
- Jones, P. L., Ryan, M. J., Flores, V. & Page, R. A. (2013). When to approach novel prey cues? Social learning strategies in frog-eating bats. *Proceedings of the Royal Society B-Biological Sciences*, 280,
- Kameda, T. & Nakanishi, D. (2002). Cost-benefit analysis of social/cultural learning in a nonstationary uncertain environment - An evolutionary simulation and an experiment with human subjects. *Evolution and Human Behavior*, 23(5), 373-393.
- Kameda, T. & Nakanishi, D. (2003). Does social/cultural learning increase human adaptability? Rogers's question revisited. *Evolution and Human Behavior*, 24(4), 242-260. Doi 10.1016/S1090-5138(03)00015-1
- Kendal, R. L., Coolen, I. & Laland, K. N. (2004). The role of conformity in foraging when personal and social information conflict. *Behavioral Ecology*, 15(2), 269-277. Doi 10.1093/Beheco/Arh008
- Kendal, R. L., Coolen, I. & Laland, K. N. 2009 Adaptive trade-offs in the use of social and personal information. In R. Dukas and J. Ratcliffe (Eds.), *Cognitive ecology II* (pp. 249-271). Chicago: University of Chicago Press.
- Kendal, R. L., Coolen, I., van Bergen, Y. & Laland, K. N. (2005). Trade-offs in the adaptive use of social and asocial learning. *Advances in the Study of Behavior*, Vol 35, 35, 333-379. Doi 10.1016/S0065-3454(05)35008-X
- King, A. J. & Cowlshaw, G. (2007). When to use social information: the advantage of large group size in individual decision making. *Biology Letters*, 3(2), 137-139. 10.1098/Rsbl.2007.0017

- Kobayashi, Y. & Ohtsuki, H. (2014). Evolution of social versus individual learning in a subdivided population revisited: Comparative analysis of three coexistence mechanisms using the inclusive-fitness method. *Theoretical Population Biology*, 92, 78-87.
- Konopasky, R. J. & Telegdy, G. A. (1977). Conformity in the rat: a leader's selection of door color versus a learned door-color discrimination. *Perceptual and Motor Skills*, 44, 31-37.
- Krützen, M., Mann, J., Helthaus, M. R., Connor, R. C., Bejder, L. & Sherwin, W. B. (2005). Cultural transmission of tool use in bottlenose dolphins. *Proceedings of the National Academy of Sciences of the United States of America*, 102(25), 8939-8943.
- Krützen, M., van Schaik, C. & Whiten, A. (2007). The animal cultures debate: response to Laland and Janik. *Trends in Ecology & Evolution*, 22(1), 6-6. Doi 10.1016/j.tree.2006.10.011
- Krützen, M., Willems, E. P. & van Schaik, C. P. (2011). Culture and Geographic Variation in Orangutan Behavior. *Current Biology*, 21(21), 1808-1812. Doi 10.1016/J.Cub.2011.09.017
- Lachlan, R. F., Crooks, L. & Laland, K. (1998). Who follows whom? Shoaling preferences and social learning of foraging information in guppies. *Animal Behaviour*, 56, 181-190.
- Laland, K., Atton, N. & Webster, M. M. (2011). From fish to fashion: experimental and theoretical insights into the evolution of culture. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 366, 958-968. Doi 10.1098/rstb.2010.0328
- Laland, K. & Williams, K. (1997). Shoaling generates social learning of foraging information in guppies. *Animal Behaviour*, 53, 1161-1169.
- Laland, K. N. (2004). Social learning strategies. *Learning & Behavior*, 32(1), 4-14.
- Laland, K. N. & Galef, B. G. (2008). *The Question of Animal Culture*. Cambridge, MA: Harvard University Press.
- Laland, K. N. & Janik, V. M. (2006). The animal cultures debate. *Trends in Ecology & Evolution*, 21(10), 542-547. Doi 10.1016/J.Tree.2006.06.005
- Laland, K. N. & Janik, V. M. (2007). Response to Krutzen et al.: Further problems with the 'method of exclusion'. *Trends in Ecology & Evolution*, 22(1), 7-7. Doi 10.1016/J.Tree.2006.10.010
- Laland, K. N., Odling-Smee, J. & Feldman, M. W. (2000). Niche construction, biological evolution, and cultural change. *Behavioral and Brain Sciences*, 23, 131-175.

- Langergraber, K., Boesch, C., Inoue, E., Inoue-Murayama, M., Mitani, J. C., Nishida, T., Pusey, A. E., Reynolds, V., Schubert, G., Wrangham, R. W., Wroblewski, E. & Vigilant, L. (2010). Genetic and 'cultural' similarity in wild chimpanzees. *Proceedings of the Royal Society B-Biological Sciences*, 277, 408-416.
- Langergraber, K., Mitani, J. & Vigilant, L. (2009). Kinship and Social Bonds in Female Chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, 71(10), 840-851. Doi 10.1002/ajp.20711
- Latané, B. & Wolf, S. (1981). The Social Impact of Majorities and Minorities. *Psychological Review*, 88(5), 438-453. Doi 10.1037//0033-295x.88.5.438
- Leadbeater, E. & Chittka, L. (2005). A new mode of information transfer in foraging bumblebees? *Current Biology*, 15, 447-448.
- Leadbeater, E. & Chittka, L. (2007). The dynamics of social learning in an insect model, the bumblebee (*Bombus terrestris*). *Behavioral Ecology and Sociobiology*, 61, 1789-1796.
- Leadbeater, E. & Chittka, L. (2007). Social Learning in Insects — From Miniature Brains to Consensus Building. *Current Biology*, 17, 703-713.
- Lefebvre, L. (1986). Cultural-Diffusion of a Novel Food-Finding Behavior in Urban Pigeons - an Experimental Field-Test. *Ethology*, 71(4), 295-304.
- Lonsdorf, E. V., Eberly, L. E. & Pusey, A. E. (2004). Sex differences in learning in chimpanzees. *Nature*, 428(6984), 715-716. Doi 10.1038/428715a
- Luncz, L. V. & Boesch, C. (2014). Tradition over Trend: Neighboring chimpanzee communities maintain differences in cultural behavior despite frequent immigration of adult females. *American Journal of Primatology*, 76(7), 649-657.
- Luncz, L. V., Mundry, R. & Boesch, C. (2012). Evidence for Cultural Differences between Neighboring Chimpanzee Communities. *Current Biology*, 22(10), 922-926. Doi 10.1016/J.Cub.2012.03.031
- Lycett, S. J., Collard, M. & McGrew, W. C. (2010). Are Behavioral Differences Among Wild Chimpanzee Communities Genetic Or Cultural? An Assessment Using Tool-Use Data and Phylogenetic Methods. *American Journal of Physical Anthropology*, 142, 461-467.
- Lycett, S. J., Collard, M. & McGrew, W. C. (2010). Correlations between genetic and behavioural dissimilarities in wild chimpanzees (*Pan troglodytes*) do not undermine the case for culture. *Proceedings of the Royal Society B-Biological Sciences*, 278, 2091-2093.

- Lyons, D. E., Young, A. G. & Keil, F. C. (2007). The hidden structure of overimitation. *Proceedings of the National Academy of Sciences*, 50, 19751-19756. Doi: 10.1073_pnas.0704452104.
- Macarthur, R. H. & Pianka, E. R. (1966). On Optimal Use of a Patchy Environment. *American Naturalist*, 100(916), 603-609.
- MacLean, E. L., Matthews, L. J., Hare, B. A., Nunn, C. L., Anderson, R. C., Aureli, F., Brannon, E. M., Call, J., Drea, C. M., Emery, N. J., Haun, D. B. M., Herrmann, E., Jacobs, L. F., Platt, M. L., Rosati, A. G., Sandel, A. A., Schroepfer, K. K., Seed, A. M., Tan, J. Z., van Schaik, C. P. & Wobber, V. (2012). How does cognition evolve? Phylogenetic comparative psychology. *Animal Cognition*, 15(2), 223-238. Doi 10.1007/S10071-011-0448-8
- Maestriperi, D. 2012 Comparative primate psychology. In *Encyclopedia of Human Behavior* (ed. V. S. Ramachandran), pp. 550-555. Amsterdam, Elsevier.
- Manrique, H. M., Volter, C. J. & Call, J. (2012). Repeated innovation in chimpanzees. *Animal Behaviour*, 1-8. Doi 10.1016/j.anbehav.2012.10.026
- Marshall-Pescini, S. & Whiten, A. (2008). Chimpanzees (*Pan troglodytes*) and the question of cumulative culture: an experimental approach. *Animal Cognition*, 11(3), 449-456. Doi 10.1007/s10071-007-0135-y
- Martin, P. & Bateson, P. (2007). *Measuring Behaviour: An Introductory Guide*. Cambridge: Cambridge University Press.
- McElreath, R., Lubell, M., Richerson, P. J., Waring, T. M., Baum, W., Edsten, E., Efferson, C. & Paciotti, B. (2005). Applying evolutionary models to the laboratory study of social learning. *Evolution and Human Behavior*, 26(6), 483-508. Doi 10.1016/J.Evolhumbehav.2005.04.003
- McElreath, R. & Strimling, P. (2008). When natural selection favors imitation of parents. *Current Anthropology*, 49, 307-316.
- Mcfarland, D. J. (1977). Decision-Making in Animals. *Nature*, 269(5623), 15-21.
- McGrew, W. C. (1974). Tool use by wild chimpanzees in feeding upon driver ants. *Journal of Human Evolution*, 3, 501-508.
- McGrew, W. C. (1992). *Chimpanzee Material Culture: Implications for Human Evolution*. Cambridge: Cambridge University Press.
- McGrew, W. C. (1998). Culture in nonhuman primates? *Annual review of anthropology*, 27, 301-328.
- McGrew, W. C. (2004). *The cultured chimpanzee: Reflections on cultural primatology*. Cambridge: Cambridge University Press

- McGrew, W. C., Marchant, L. F., Scott, S. E. & Tutin, C. E. G. (2001). Intergroup differences in a social custom of wild chimpanzees: The grooming hand-clasp of the Mahale Mountains. *Current Anthropology*, 42(1), 148-153.
- McGrew, W. C. & Tutin, C. E. G. (1978). Evidence for a Social Custom in Wild Chimpanzees? *Man*, 13(2), 234-251.
- McGuigan, N., Makinson, J. & Whiten, A. (2011). From over-imitation to super-copying: adults imitate causally irrelevant aspects of tool use with higher fidelity than young children. *British Journal of Psychology*, 102, 1-18. Doi 10.1348/000712610X493115.
- Mery, F., Varela, S. A. M., Danchin, E., Blanchet, S., Parejo, D., Coolen, I. & Wagner, R. H. (2009). Public Versus Personal Information for Mate Copying in an Invertebrate. *Current Biology*, 19, 730-734.
- Mesoudi, A. (2007). Using the methods of experimental social psychology to study cultural evolution. *Journal of Social, Evolutionary, and Cultural Psychology*, 1(2), 35-58.
- Mesoudi, A. (2009). How Cultural Evolutionary Theory Can Inform Social Psychology and Vice Versa. *Psychological Review*, 116(4), 929-952. Doi 10.1037/0017062
- Mesoudi, A. (2011). *Cultural Evolution: how Darwinian theory can explain human culture & synthesize the social sciences*. London: University of Chicago Press.
- Mitani, J. C. (2009). Male chimpanzees form enduring and equitable social bonds. *Animal Behaviour*, 77(3), 633-640. Doi 10.1016/j.anbehav.2008.11.021
- Möbius, Y., Boesch, C., Koops, K., Matsuzawa, T. & Humle, T. (2008). Cultural differences in army ant predation by West African chimpanzees? A comparative study of microecological variables. *Animal Behaviour*, 76, 37-45.
- Moore, R. (2013). Social learning and teaching in chimpanzees. *Biology & Philosophy*, 28(6), 879-901. Doi 10.1007/s10539-013-9394-y
- Morgan, T. J. H. & Laland, K. (2012). The biological bases of conformity. *Frontiers in Neuroscience*, 6(87). Doi 10.3389/fnins.2012.00087
- Morgan, T. J. H., Rendell, L., Ehn, W., Hoppitt, W. & Laland, K. (2011). The evolutionary basis of human social learning. *Proceedings of the Royal Society B-Biological Sciences*. Doi 10.1098/rspb.2011.1172
- Mundinger, P. C. 1982 Microgeographic and macrogeographic variation in birds. In D. E. Kroodsma, E. H. Miller and H. Ouellet (Eds.), *Acoustic Communication in Birds* (pp. 147-208). New York: Academic Press.

- Muthukrishna, M., Shulman, B. W., Vasilescu, V. & Henrich, J. (2014). Sociality influences cultural complexity. *Proceedings of the Royal Society B-Biological Sciences*, 281. Doi 10.1098/rspb.2013.2511
- Nakahashi, W., Wakano, J. Y. & Henrich, J. (2012). Adaptive social learning strategies in temporally and spatially varying environments. *Human Nature*, 23, 386-418.
- Nakamura, M., McGrew, W. C., Marchant, L. F. & Nishida, T. (2000). Social Scratch: Another Custom in Wild Chimpanzees? *Primates*, 41(3), 237-248.
- Nakamura, M. & Uehara, S. (2004). Proximate factors of different types of grooming hand-clasp in mahale chimpanzees: Implications for chimpanzee social customs. *Current Anthropology*, 45(1), 108-114.
- Nicol, C. J. (2004). Development, direction, and damage limitation: Social learning in domestic fowl. *Learning & Behavior*, 32, 72-81.
- Nielsen, M., Subiaul, F., Whiten, A., Galef, B. G. & Zentall, T. (2012). Social Learning in Humans and Nonhuman Animals: Theoretical and Empirical Dissections. *Journal of Comparative Psychology*, 126(2), 109-113.
- Over, H. & Carpenter, M. (2011). Putting the Social Into Social Learning: Explaining Both Selectivity and Fidelity in Children's Copying Behavior. *Journal of Comparative Psychology*. Doi 10.1037/a0024555
- Payne, R. B. (1985). Behavioral Continuity and Change in Local Song Populations of Village Indigobirds *Vidua-Chalybeata*. *Zeitschrift Fur Tierpsychologie-Journal of Comparative Ethology*, 70(1), 1-44.
- Perreault, C., Moya, C. & Boyd, R. (2012). A Bayesian approach to the evolution of social learning. *Evolution and Human Behavior*, 33, 449-459. Doi 10.1016/j.evolhumbehav.2011.12.007
- Perry, S. (2009). Conformism in the food processing techniques of white-faced capuchin monkeys (*Cebus capucinus*). *Animal Cognition*, 12(5), 705-716. Doi 10.1007/S10071-009-0230-3
- Perry, S., Baker, M., Fedigan, L., Gros-Louis, J., Jack, K., MacKinnon, K. C., Manson, J. H., Panger, M., Pyle, K. & Rose, L. (2003). Social conventions in wild white-faced capuchin monkeys - Evidence for traditions in a neotropical primate. *Current Anthropology*, 44(2), 241-268. Doi 10.1086/345825
- Pesendorfer, M. B., Gunhold, T., Schiel, N., Souto, A., Huber, L. & Range, F. (2009). The Maintenance of Traditions in Marmosets: Individual Habit, Not Social Conformity? A Field Experiment. *Plos One*, 4(2). Doi 10.1371/journal.pone.0004472

- Pike, T. W. & Laland, K. N. (2010). Conformist learning in nine-spined sticklebacks' foraging decisions. *Biology Letters*, 6(4), 466-468. Doi 10.1098/Rsbl.2009.1014
- Pradhan, G. R., Tennie, C. & van Schaik, C. P. (2012). Social organization and the evolution of cumulative technology in apes and hominins. *Journal of Human Evolution*, 63(1), 180-190.
- Price, E. E., Lambeth, S. P., Schapiro, S. J. & Whiten, A. (2009). A potent effect of observational learning on chimpanzee tool construction. *Proceedings of the Royal Society B-Biological Sciences*, 276(1671), 3377-3383. Doi 10.1098/rspb.2009.0640
- Price, E. E. & Whiten, A. 2012 Social Learning and Culture in Primates: Evidence from Free-Ranging and Captive Populations. In T. Zentall and E. Wasserman (Eds.), *Handbook of Comparative Cognition*. Oxford: Oxford University Press.
- Reader, S. M. & Biro, D. (2010). Experimental identification of social learning in wild animals. *Learning & Behavior*, 38(3), 265-283.
- Reader, S. M. & Hrotic, S. M. (2012). The limits of chimpanzee-human comparisons for understanding human cognition. Response to: The cognitive bases of human tool use by Krist Vaesen. *Behavioral and Brain Sciences*, 35, 238-239.
- Rendell, L., Boyd, R., Cownden, D., Enquist, M., Eriksson, K., Feldman, M. W., Fogarty, L., Ghirlanda, S., Lillicrap, T. & Laland, K. N. (2010). Why Copy Others? Insights from the Social Learning Strategies Tournament. *Science*, 328(5975), 208-213. Doi 10.1126/Science.1184719
- Rendell, L., Fogarty, L., Hoppitt, W. J. E., Morgan, T. J. H., Webster, M. M. & Laland, K. N. (2011). Cognitive culture: theoretical and empirical insights into social learning strategies. *Trends in Cognitive Sciences*, 15(2), 68-76.
- Rendell, L., Fogarty, L. & Laland, K. N. (2010). Rogers' Paradox Recast and Resolved: Population Structure and the Evolution of Social Learning Strategies. *Evolution*, 64(2), 534-548. Doi 10.1111/J.1558-5646.2009.00817.X
- Rendell, L. & Whitehead, H. (2001). Culture in whales and dolphins. *Behavioral and Brain Sciences*, 24(2), 309-382. Doi 10.1017/S0140525x0100396x
- Richerson, P. (2013). Group size determines cultural complexity. *Nature*, 503, 351-352. Doi 10.1038/nature12708
- Richerson, P. J. & Boyd, R. (2005). *Not by genes alone: how culture transformed human evolution*. Chicago: The University of Chicago Press.

- Rieucau, G. & Giraldeau, L. A. (2011). Exploring the costs and benefits of social information use: an appraisal of current experimental evidence. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 366, 949-957. Doi 10.1098/rstb.2010.0325
- Rogers, A. R. (1988). Does Biology Constrain Culture? *American Anthropologist*, 90(4), 819-831.
- Ron, T. & McGrew, B. (1988). Ecological assessment for a chimpanzee rehabilitation project in Northern Zambia. *Primate Conservation*, 9, 37-41.
- Rosa, P., Nguyen, V. & Dubois, F. (2012). Individual differences in sampling behaviour predict social information use in zebra finches. *Behavioral Ecology and Sociobiology*, 66, 1259-1265. Doi 10.1007/s00265-012-1379-3
- Sanz, C. M., Schöning, C. & Morgan, D. B. (2009). Chimpanzees Prey on Army Ants with Specialized Tool Set. *American Journal of Primatology*, 71, 1-8.
- Schlag, K. H. (1998). Why imitate, and if so, how? A boundedly rational approach to multi-armed bandits. *Journal of Economic Theory*, 78(1), 130-156.
- Schöning, C., Humle, T., Möbius, Y. & McGrew, W. C. (2008). The nature of culture: technological variation in chimpanzee predation on army ants. *Journal of Human Evolution*, 55, 48-59.
- Schrauf, C., Call, J., Fuwa, K. & Hirata, S. (2012). Do Chimpanzees Use Weight to Select Hammer Tools? *Plos One*, 7(7). Doi 10.1371/journal.pone.0041044_ARTN e41044
- Sherif, M. (1936). *The psychology of social norms*. Oxford, England: Harper.
- Starkweather, E. K. (1970). *Starkweather Social Conformity Test for Preschool Children*. Stillwater, OK: Oklahoma State University.
- Sterelny, K. (2006). The Evolution and Evolvability of Culture. *Mind & Language*, 21(2), 137-165.
- Strimling, P., Enquist, M. & Eriksson, K (2009) Repeated learning makes cultural evolution unique. *Proceedings of the National Academy for Sciences*, 33, 13870-13874. Doi 10.1073 / pnas.0903180106
- Sugiyama, Y. (1995). Tool-use for catching ants by chimpanzees at Bossou and Monts Nimba, West Africa. *Primates*, 36, 193-205.
- Tacchetti, M., van Leeuwen, E. J. C., Haun, D. B. M. & Cronin, K. A. (In preparation). Chimpanzees use gestures to coordinate social grooming interactions.

- Tanford, S. & Penrod, S. (1984). Social-Influence Model - a Formal Integration of Research on Majority and Minority Influence Processes. *Psychological Bulletin*, 95(2), 189-225. Doi 10.1037//0033-2909.95.2.189
- Team, R. D. C. (2011). *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Tennie, C., Call, J. & Tomasello, M. (2009). Ratcheting up the ratchet: on the evolution of cumulative culture. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 364(1528), 2405-2415. Doi 10.1098/rstb.2009.0052
- Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift für Tierpsychologie*, 20, 410-433.
- Toelch, U., Bruce, M. J., Newson, L., Richerson, P. J. & Reader, S. M. (2014). Individual consistency and flexibility in human social information use. *Proceedings of the Royal Society B-Biological Sciences*, 281. Doi 10.1098/rspb.2013.2864
- Tomasello, M. (1999). *The Cultural Origins of Human Cognition*. Cambridge, MA.: Harvard University Press.
- Tomasello, M. (1999). The human adaptation for culture. *Annual review of anthropology*, 28, 509-529.
- Ulvestad, E. (2007). *Defending life: the nature of host-parasite relations*. Dordrecht: Springer.
- van Bergen, Y., Coolen, I. & Laland, K. (2004). Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. *Proceedings of the Royal Society B-Biological Sciences*, 271, 957-962. Doi 10.1098/rspb.2004.2684
- van de Waal, E., Borgeaud, C. & Whiten, A. (2013). Potent Social Learning and Conformity Shape a Wild Primate's Foraging Decisions. *Science*, 340, 483-485. Doi 10.1126/science.1232769
- van den Bos, R., Jolles, J. W. & Homberg, J. R. (2013). Social modulation of decision-making: a cross-species review. *Frontiers in Human Neuroscience*, 7(301), 1-16. Doi 10.3389/fnhum.2013.00301
- van Schaik, C. P. (1983). Why are diurnal primates living in groups? *Behaviour*, 87, 120-144.
- van Schaik, C. P. (2012). Animal Culture: Chimpanzee Conformity? *Current Biology*, 22(10), R402-R404. Doi 10.1016/J.Cub.2012.04.001

- van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I., Suzuki, A., Utami, S. S. & Merrill, M. (2003). Orangutan cultures and the evolution of material culture. *Science*, 299(5603), 102-105. Doi 10.1126/Science.1078004
- Volter, C. J. & Call, J. (2012). Problem solving in great apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, and *Pongo abelii*): the effect of visual feedback. *Animal Cognition*, 15, 923-936. Doi 10.1007/s10071-012-0519-5
- Wakano, J. Y. & Aoki, K. (2007). Do social learning and conformist bias coevolve? Henrich and Boyd revisited. *Theoretical Population Biology*, 72(4), 504-512. Doi 10.1016/J.Tpb.2007.04.003
- Walker, M. B. & Andrade, M. G. (1996). Conformity in the Asch task as a function of age. *Journal of Social Psychology*, 136(3), 367-372.
- Wallace, A. R. (1858). On the tendency of varieties to depart indefinitely from the original type. Ternate: Linnean Society.
- Webster, M. M. & Hart, P. J. B. (2006). Subhabitat selection by foraging threespine stickleback (*Gasterosteus aculeatus*): previous experience and social conformity. *Behavioral Ecology and Sociobiology*, 60(1), 77-86. Doi 10.1007/S00265-005-0143-3
- Webster, T. H., Hodson, P. R. & Hunt, K. D. (2009). Grooming hand-clasp by chimpanzees of the Mugiri community, Toro-Semliki Wildlife Reserve, Uganda. *Pan Africa News*, 16(1), 5-7.
- Webster, T. H., Hodson, P. R. & Hunt, K. D. (2009). Grooming hand-clasp by chimpanzees of the Mugiri community, Toro-Semliki Wildlife Reserve, Uganda. *Pan Africa News*, 16(1), Unpaginated.
- Whiten, A. (1998). Imitation of the sequential structure of actions by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 112(3), 270-281. Doi 10.1037/0735-7036.112.3.270
- Whiten, A. (2003). Response to: S. Perry et al. 2003 Social conventions in wild white-faced capuchin monkeys - Evidence for traditions in a neotropical primate. *Current Anthropology*, 44, 260-261.
- Whiten, A. (2005). The second inheritance system of chimpanzees and humans. *Nature*, 437(7055), 52-55. Doi 10.1038/nature04023
- Whiten, A. (2011). The scope of culture in chimpanzees, humans and ancestral apes. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 366, 997-1007.

- Whiten, A. & Erdal, D. (2012). The human socio-cognitive niche and its evolutionary origins. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 367, 2119-2129.
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W. & Boesch, C. (1999). Cultures in chimpanzees. *Nature*, 399(6737), 682-685. Doi 10.1038/21415
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W. & Boesch, C. (2001). Charting cultural variation in chimpanzees. *Behaviour*, 26, 1481-1516.
- Whiten, A. & Ham, R. (1992). On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research. *Advances in the Study of Behavior*, 11, 239-283.
- Whiten, A., Horner, V. & de Waal, F. B. M. (2005). Conformity to cultural norms of tool use in chimpanzees. *Nature*, 437(7059), 737-740. Doi 10.1038/nature04047
- Whiten, A., Horner, V. & Marshall-Pescini, S. (2003). Cultural Panthropology. *Evolutionary Anthropology*, 12(2), 92-105. Doi 10.1002/evan.10107
- Whiten, A. & Mesoudi, A. (2008). Establishing an experimental science of culture: animal social diffusion experiments. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 363(1509), 3477-3488. Doi 10.1098/Rstb.2008.0134
- Whiten, A., Spiteri, A., Horner, V., Bonnie, K. E., Lambeth, S. P., Schapiro, S. J. & de Waal, F. B. M. (2007). Transmission of multiple traditions within and between chimpanzee groups. *Current Biology*, 17(12), 1038-1043. Doi 10.1016/J.Cub.2007.05.031
- Whiten, A. & van Schaik, C. P. (2007). The evolution of animal 'cultures' and social intelligence. *Royal Society Philosophical Transactions Biological Sciences*, 362(1480), 603-620.
- Whiten, A. & van Schaik, C. P. (2007). The evolution of animal 'cultures' and social intelligence. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 362(1480), 603-620. Doi 10.1098/rstb.2006.1998
- Wood, L. A., Kendal, R. L. & Flynn, E. G. (2012). Context-dependent model-based biases in cultural transmission: children's imitation is affected by model age over model knowledge state. *Evolution and Human Behavior*, 33, 387-394. Doi 10.1016/j.evolhumbehav.2011.11.010
- Wood, L. A., Kendal, R. L. & Flynn, E. G. (2013). Copy me or copy you? The effect of prior experience on social learning. *Cognition*, 127, 203-213. Doi 10.1016/j.cognition.2013.01.002

- Wolf, M., Kurvers, R. H. J. M., Ward, A. J. W., Krause, S. & Krause, J. (2013). Accurate decisions in an uncertain world: collective cognition increases true positives while decreasing false positives. *Proceedings of the Royal Society B-Biological Sciences*, 280. Doi 10.1098/rspb.2012.2777
- Wrangham, R. W., de Waal, F. B. M. & McGrew, W. C. 1994 The Challenge of Behavioral Diversity. In R. W. Wrangham, W. C. McGrew, F. B. M. de Waal and P. G. Heltne (Eds.), *Chimpanzee Cultures* (pp. 1-18). Cambridge, Massachusetts: Harvard University Press.
- Yamamoto, S., Humle, T. & Tanaka, M. (2013). Basis for cumulative cultural evolution in chimpanzees: social learning of a more efficient tool-use technique. *Plos One*, 8(1), e55768

Samenvatting

In dit proefschrift heb ik chimpansees onderzocht met als doel om primatengedrag beter te begrijpen en daarmee dus ook menselijk gedrag. Aan de ene kant kan het bestuderen van de manieren waarop andere sociale dieren hun leven inrichten en hoe die manieren van invloed zijn op de wisselwerking tussen gedrag en omgeving ons inzicht geven in de vele vormen en functies van evolutionaire processen. Aan de andere kant kan de studie van chimpansees ons iets vertellen over onze evolutionaire blauwdruk aangezien ze onze nauwste nog levende verwanten zijn (samen met de bonobo). Met andere woorden, als we een bepaald menselijk gedrag ook terugzien bij de chimpansee, dan kunnen we er vanuit gaan dat dit gedrag evolutionair gezien vrij oud is en dat het betreffende gedrag dus niet iets is wat mensen pas ontwikkeld hebben nadat ze waren afgesplitst van de andere mensapen. Naast het feit dat we door middel van zulke vergelijkende studies een beter zicht krijgen op de omstandigheden waarin bepaalde gedragingen ontstaan, kan dergelijke kennis ons ook informeren over de mate waarin gedrag verankerd ligt in onze (instinctieve) drijfveren. Het lijkt namelijk zo te zijn dat dieren, inclusief wij mensen, niet oneindig flexibel zijn in hun gedrag, maar integendeel een neiging hebben om 'in het verleden behaalde resultaten' mee te nemen in de beslissingen van vandaag.

Kort gezegd heb ik me in dit proefschrift gericht op het onderzoeken van culturele uitingen in het leven van chimpansees, zowel met betrekking tot *functie* (wat betekenen deze uitingen precies voor de chimpansees?) als *vergelijkende studie* (in welke mate komen de culturele uitingen van chimpansees overeen met die van mensen?). Hieronder volgt een beknopt overzicht van de projecten waaraan ik heb gewerkt in het licht van bovengenoemde thema's.

Hebben chimpansees ook cultuur?

Om te weten te komen of chimpansees cultuur hebben nam ik een strikte definitie van cultuur zoals die is voortgekomen uit recente wetenschappelijke debatten (Perry et al., 2003; Whiten, 2003) en onderzocht vervolgens of de

gedragingen van vier chimpansee gemeenschappen daar eventueel aan voldeden. In hoofdstuk 2 heb ik gekeken naar een speciaal soort vlooi-gedrag wat zich het beste laat omschrijven de 'vlooi-handdruk' (de 'grooming hand-clasp', zie McGrew & Tutin, 1978). Dit project werd uitgevoerd in een Zambiaans opvangcentrum genaamd 'Chimfunshi', waar vier stabiele groepen chimpansees leven onder semi-wilde omstandigheden (ze eten en slapen buiten in Miombo bos). De vlooi-handdruk (VHD) is een specifieke vlooi houding waarbij twee chimpansees elkaars handen pakken, deze de lucht in steken, en vervolgens elkaar vlooiën met hun andere (nog vrije) hand. De VHD bleek uniek te zijn voor één bepaalde groep chimpansees (een wilde groep in de Mahale bergen in Tanzania), als zodanig dus geen onderdeel uit te maken van het typische, aangeboren gedragsrepertoire van chimpansees en werd uiteindelijk om die reden beschouwd als een cultureel overgedragen eigenschap (zie McGrew & Tutin, 1978; Whiten et al., 2001). Echter, na verloop van tijd bleek de VHD toch op te duiken in een toenemend aantal wilde en beheerde chimpansee populaties en aldus verloor het zijn oorspronkelijke status van niet-menselijke cultuur. Mijn eerste project herwint iets van de oorspronkelijke 'cultuur claim': Ik laat zien dat chimpansees groep-specifieke stijlen gebruiken waarmee ze de VHD ten uitvoer brengen. Deze groep-specifieke voorkeursstijlen werden gedeeld door alle leden van de groep, waren stabiel over drie punten in de tijd (2007, 2010 en 2011) en konden niet (voldoende) verklaard worden door ecologische, genetische en/of fenotypische factoren. In het licht van deze nieuwe bevindingen concludeerde ik dat de VHD tóch een sociaal-overdraagbare eigenschap is met kenmerken die doen denken aan menselijke cultuur (van Leeuwen et al., 2012).

In hoofdstuk 3 heb ik onderzocht of chimpansees ook geneigd zijn om *willekeurig* gedrag van hun groepsleden te kopiëren. Deze bevinding zou een extra indicatie zijn dat chimpansees culture gedragsvormen hebben, bovenop het beschreven VHD gedrag wat toch een nauwe link heeft met daadwerkelijk *functioneel* gedrag (vlooiën). Met andere woorden, zouden chimpansees ook arbitrair gedrag kopiëren in een soortgelijke manier als mensen modetrends volgen? Net als in hoofdstuk 2 bestudeerde ik de vier groepen half-wilde chimpansees in Chimfunshi. Door het analyseren van systematisch verkregen video opnames (±720 uur) vond ik dat één chimpansee regelmatig gras in haar

oren stopte zonder dat daar een directe reden voor leek te zijn (Julie). Bij nadere beschouwing bleek dat gaandeweg 7 van haar groepsgenoten dit gedrag overnamen en dat er aldus een klein 'gras-in-oor gedrag' (GIO) cultuurtje ontstond. De video's lieten zien dat dit gedrag zich in geen enkele andere groep voordeed. Bovendien zag ik dat de 7 na-apers zich allemaal eerst goed oriënteerden op de uitvinder van het gedrag alvorens ze zelfs gras in hun oren gingen stoppen. Met andere woorden, alles leek erop te wijzen dat de chimpansees daadwerkelijk van elkaar leerden, wat een centraal aspect is van elke vorm van (menselijke) 'cultuur'.

Zijn chimpansees gevoelig voor groepsdruk?

Om de reden dat conformiteit (aan de meerderheid van de groep) wordt gezien als een van de drijvende krachten achter de vorming van cultuur (i.e., het ontstaan van groepsverschillen, zie Richerson & Boyd, 2005), ben ik vervolgens gaan onderzoeken of conformiteit ook voorkomt in het gedragspatroon van chimpansees. Met andere woorden, zou het zo kunnen zijn dat chimpansees culturele groepsverschillen hebben doordat zij zich conformeren aan de meerderheid binnen hun respectievelijke groepen? Allereerst heb ik in hoofdstuk 4 de huidige overtuiging dat conformiteit reeds is aangetoond bij chimpansees (zie Whiten et al., 2005; Hopper et al., 2011; Claidière & Whiten, 2012) kritisch onderzocht. Met behulp van een methodologische analyse heb ik bepleit dat het bewijs tot nu toe niet overtuigend is en dat de chimpansees in de betreffende studies wellicht hebben gehandeld uit een neiging tot conservatisme in plaats van conformiteit (van Leeuwen & Haun, 2013). In hoofdstuk 5 heb ik deze hypothese vervolgens empirisch onderzocht. Door middel van het bestuderen van een groep chimpansees in het Wolfgang Köhler Primate Research Center (Leipzig, Duitsland) en een groep chimpansees in Chimfunshi toonde ik aan dat wanneer de motivatie tot conservatisme en conformiteit tegen elkaar worden afgezet, chimpansees zich eerder conservatief opstellen dan conform de meerderheid te handelen. Als een positieve controle en verdere analyse van chimpansees' flexibiliteit heb ik vervolgens de neiging tot conservatisme afgezet tegen de mogelijkheid om hogere beloningen te verkrijgen. In dit specifieke scenario observeerde ik dat chimpansees hun vertrouwde gedrag laten varen en

zichzelf een andere strategie aanmeten, de meest lucratieve strategie. Aldus concludeerde ik dat chimpansees zich niet snel schikken naar de meerderheid van de groep, maar dat ze hun vertrouwde gedrag wel degelijk kunnen aanpassen mits ze erop vooruit gaan in termen van netto beloningen (van Leeuwen et al., 2013).

De relatieve waarde van sociale informatie

De sociale overdracht van informatie is een cruciaal kenmerk van elke definitie van cultuur. Om een dergelijke transmissie te faciliteren dienen individuen sociale informatie te herkennen en integreren in hun eigen gedrag. Mijn laatste project draaide om de relatieve waarde die chimpansees en kinderen toekennen aan sociale informatie, geoperationaliseerd als de mate waarin zij relevante sociale informatie in aanwezigheid van even relevante individuele informatie verkiezen. Allereerst heb ik me echter gericht op het belangrijke onderscheid tussen sociale- en meerderheids-invloeden. Aldus heb ik in hoofdstuk 6 alle vermeende conformiteitsbevindingen in het dierenrijk onderzocht in het licht van dit onderscheid. In navolging van de primaten focus in hoofdstuk 4 toonde ik in hoofdstuk 6 aan dat veel van deze conformiteitsbevindingen alternatief verklaard kunnen worden, in dit geval door een waardering van de intrinsieke kracht van sociale informatie. Met andere woorden, in de meeste gevallen bleek het effect wat slechts één individu kan hebben op de observeerder niet als graadmeter te zijn gebruikt om het effect van de meerderheid te duiden. In een poging om de studie van sociale invloeden beter te stroomlijnen opperde ik verschillende methodologische verbeteringen zoals het integreren van een proces van differentiaal diagnostiek (welke sociale invloeden spelen tegelijkertijd een rol en hoe kunnen die los van elkaar worden bestudeerd?), het aanvullen van meerderheidsmanipulaties met experimentele manipulaties waarbij slechts één soortgenoot de informatie overbrengt en het kwantificeren van de afstand tussen het oorspronkelijke gedrag van het betreffende individu en het gedrag wat uitgedragen wordt door de meerderheid van de groep. Vervolgens wordt in hoofdstuk 7 het empirische onderzoek naar informatiebron voorkeuren van chimpansees en 3-4 jaar oude kinderen beschreven. Ik bedacht een experimentele procedure waarin chimpansees en

kinderen gelijkwaardige individuele en sociale kennis (gedemonstreerd door één soortgenoot) over de locatie van een beloning opdeden. De volgorde waarin individuele en sociale informatie werd verkregen was verschillend zodat ongeveer de helft van de chimpansees en kinderen eerst individuele informatie kreeg en de andere helft eerst sociale informatie. Daarnaast participeerde ieder individu in twee onafhankelijke condities: in de ene conditie werd al na 2 minuten getest welke informatiebron werd gevolgd in de uiteindelijke voorkeurstest, terwijl in de andere conditie deze voorkeurstest pas na 24 uur plaatsvond. Uiteindelijk observeerde ik dat zowel de chimpansees als de kinderen vooral een beroep deden op hun individueel verworven kennis, ongeacht de tijd tussen informatieverwerving en de voorkeurstest. Echter, in de gevallen waarin de individuen eerst sociale informatie verkregen bleken vooral kinderen geneigd te zijn deze informatie te gebruiken bij hun volgende, individuele informatieverwerving, niet de chimpansees. Ik concludeerde dat een algemene voorspelling over informatiegebruik in dieren werd bevestigd (individuele informatie, *ceteris paribus*, verdient de voorkeur boven sociale informatie; b.v., zie Richerson & Boyd, 2005; Kendal et al., 2009), en dat kinderen meer geneigd zijn om sociale informatie te gebruiken wanneer ze nog geen relevante individuele informatie hebben opgedaan dan chimpansees. Deze laatste bevinding heb ik vervolgens in verband gebracht met het ogenschijnlijk grote verschil in culturele proliferatie tussen mensen en chimpansees (zie Mesoudi, 2011).

Conclusies

Samengevat suggereren mijn bevindingen dat de gedragspatronen van chimpansees niet alleen gestoeld zijn op genetische aanleg en idiosyncratische neigingen, maar ook op sociale leerprocessen die kunnen leiden tot groep-specifieke tradities. Deze tradities kunnen worden gevormd rond soort-specifiek gedrag zoals sociaal vlooi-gedrag (hoofdstuk 2), maar ook rondom willekeurige, schijnbaar niet-functionele handelingen zoals het stoppen van gras in oren (hoofdstuk 3). Gericht op het begrijpen van de manier waarop chimpansees uiteindelijk convergeren op specifieke tradities heb ik analytisch (hoofdstuk 4) en empirisch (hoofdstuk 5) getest of chimpansees gevoelig zijn voor groepsdruk.

Het bleek dat hoewel in staat om hun gedrag aan te passen voor hogere beloningen, chimpansees zich niet laten leiden door wat de meerderheid van de groep doet, zelfs niet als ze zichzelf als minderheid kunnen waarnemen. Voortbordurend op de mogelijke rol van het gedrag van soortgenoten in de beslissingen die dieren (inclusief mensen) nemen, heb ik vervolgens gepleit voor een striktere afbakening van sociale- en meerderheidsinvloeden met als doel het verhogen van empirische nauwkeurigheid (hoofdstuk 6). Waar sociale- en meerderheidsinvloeden vaak met elkaar worden verward, heb ik me gericht op het ophelderen van het feit dat sociale informatie een vector is met een bijbehorende waarde, en dat deze waarde afhankelijk is van individuele-, sociale- en omgevingsfactoren, gemedieerd door selectiedruk en leerervaringen. Gevoed door dit principe heb ik de informatievoorkeuren van chimpansees en kinderen onderzocht en observeerde dat beide soorten voornamelijk vertrouwden op individuele informatie. Echter, wanneer de individuen nog geen individuele informatie tot hun beschikking hadden over de contingenties van de omgeving bleken kinderen duidelijk meer geneigd om sociale informatie te gebruiken dan chimpansees (hoofdstuk 7). Waar deze bevindingen reeds waardevolle inzichten opleveren voor soort-specifieke gedragstendenties kunnen ze bovendien helpen verklaren waarom mensen en chimpansees verschillen in hun culturele proliferatie en licht werpen op welke (sociale) factoren de motivatie kunnen veroorzaken om te leren van anderen.

Acknowledgements

My supervisors Daniel and Katie have been indispensable during my PhD work. Both of you have always believed in me, for which I will be forever grateful.

Dear Katie, you recommended me to Daniel after only knowing me for 6 weeks. Your faith in me brought me to be able to live my dream, after a years-long search. You inspired me and patiently encouraged me to develop my thoughts into more concrete forms. For all the interesting chats, thought-provoking dialogues, and great fun we had: Twatotela sana, a hundred percent.

Dear Dan, many thanks for trusting Katie in her recommendation. From the moment I met you, you were an ideal supervisor for me: Relaxed, fun and to the point. You have always been supportive of my ideas and provided stimulating avenues for me explore. Many thanks for your trust, your support, and your looking out for me – I'm excited for many more collaborative years to come.

My promotor Steve, many thanks for your enthusiasm for my research and for hosting me so warmly in your institute. I have learned a lot from your perspectives on culture and your meticulous writing-style analysis.

The Comparative Cognitive Anthropology group – how I wished we were all in the same place. The times we *were* together, it was great fun, and your collective enthusiasm for all the topics under study fuelled me with lots of positive energy for my own projects. Dear Antje, Emma, Henriette, Marie, Nadja, Sandy, Yvonne – thank you for your thoughts and smiles, I hope these words find you well.

Dear Zeb, a special thanks to you, for all your time and efforts spent on my projects, for your persistence while Fraukje and Dorien were spitting in your face incessantly, for your inspiring optimism and friendship. I am very happy to find you next to me as my paranymp.

The Coding Team in Nijmegen, you have been key to gaining an understanding of the social lives of the Chimfunshi chimpanzees – without you, their lives would still be hidden in tons of megabytes. Dear Becky, Karoline, Maddalena, Marjolein, Marloes, Ruti, know that your industrious work has been very valuable, and will continue to be so in the future.

Dear Viv, a special thanks to you. With your extensive knowledge of chimpanzees, your admirable dedication, your funny stories and lovely presence, you have made the Social Climate Coding project into a big success.

The technical group at the MPI Nijmegen, especially Alex, Dick and Rick, the facilitating team Ad, Jan and Rober, and the dedicated team of secretaries Edith and Ina – many thanks for your continuous support throughout my PhD work.

The Wolfgang Köhler Primate Research Center team, dear Josep, Sebastian, Hanna, Johannes, Raik and Daniel – I’m thankful for your willingness to host my projects and for doing that with such great care and kindness. To all WKPRC chimpanzee keepers, you have been central to the execution of my projects.

My colleagues and friends from the Max Planck Institute in Leipzig, in particular Harriet, Katja and Richard, you have made me feel at home in Leipzig from the very first day onwards. I have greatly enjoyed our time together, thank you for your hospitality, your inspiring thoughts, your friendship.

Dear Roger, thank you for being a great statistical teacher, a refreshingly unbiased thinker, a good friend. The moments on the roof, the (too few) beers & burgers, the discussions on life & modelling the world – all these experiences have enriched my research time, I’m looking forward to many more to come.

Dear Colleen, Hi-C, thank you for always being willing to help me out in the R-world and for doing that with such great patience and skill. You have a gift and the way you use it makes you awesome.

Dear Chimfunshi, how you are my extended family. You are the only place I happily conform to, your pace is both exhilarating and soothing. Twatotela sana for welcoming me in your midst, and for taking care of me so well.

“The guys”, dear abanandi, you are the best. Albert, Chrispin, Clifford, Ebby, Goodson, Jackson, John, Joseph, Misheck, Mumba, Patrick, Peter, Richard, Sakala, Thom – I couldn’t have carried out my research if it wasn’t for your heartfelt dedication. Mwefibusa fyandi, Mwali abakumpeela ubwafwilisho ubwaibela ukufuma kuntendekelo nokufikafye nakuumpela Ya milimo yandi. Napali ico, kuti natemwa ukumitasha umufuma chuumi. Ukutasha ukwingi pakuipelesha kwenu, pakusakamana ba kolwe, pakunsakama nokuntangata ukuchisha panshita elyo nakwele, pakungafwilisha mu milimo yandi imo ishalolamo nokulolamo iyo iyalebombwa mukasuba aka tandemono. Cinecine mulifibusa ifyapulamo. Naliba uwakuipakisha, kaili nkatwalilila ukuipakisha nechibusa chintu mwampela, imilumbe Shenu, ukutangata kwenu ukubikapofye nechitemwiko chenu. Natutwalilile ukulila capamo kaili ukuti nakasuba Katwalilile ukubengeshima kuli imwe ne ndupwa shenu. (Priscilla, thank you for your kind help with the bemba translation).

Joyce, Patricia, Rebecca, Martha, and all the other great women of Chimfunshi – thank you for making me feel at home in the middle of the bush, and for treating me with your delicious chikanda.

Patrick Mwika, such honour that you named your son after me. Natasha sana for your unconditional help with my research projects and for sharing your free-spirited thoughts with me. Ukwikatana.

Felix, with your beautiful smile, your great demeanour around chimpanzees and people, and your unlimited readiness to help everybody around you, you truly are an inspiration to us all. Thank you for letting me play on your team, both around the chimpanzees and on the soccer-field. Nakalebalika.

Dear Sheila, thinking about the many chimpanzees that have found happiness under your family's wings – after losing it so abruptly – makes me, and should make everybody, unconditionally and inspirationally grateful.

Dear Mary, bamama, you are Chimfunshi's indispensable backbone. Thank you very much for your loving care, for all that breathes Chimfunshi. Lesa Apale.

My dear friend Innocent – I have a lot of respect and admiration for the way you empower your staff, for the way you juggle the very many tasks and demands in Chimfunshi. Here, I want to thank you wholeheartedly for always being responsive to my questions, for helping me execute crazy, muzungu-distorted research projects, for your friendship, and for going the extra mile for me. Natotela.

Sebastian, following in the commendable footsteps of your late brother Stephan, you have kept Chimfunshi afloat with your generous support. We are all very grateful for your efforts, vielen Dank, also to Cornelia, Helmut and Vitali.

Brother Mark, your spark ignited my love for Chimfunshi. You brought me to Chimfunshi and cultivated my dream, even before I knew its contents. I will be forever grateful for your indispensable role in fulfilling my life as primatologist.

The Gonzaga University and its dedicated students, especially Ben, Sam and Tom, I am much obliged for your help throughout the handclasp project.

Dear Ian, Rachael, Rosie – thank you for your support at Chimfunshi, the setting up of a volunteer (video collection) program, the great fun we had, your looking out for me.

Dear Diana, Marina and Sonja, you have been fundamental to the start of my research career. Diana, thank you for accepting me on board of your Chimfunshi adventure. Marina, thank you for offering me to take part in one of your projects.

For the first time, I experienced the thrill of unravelling non-human primate behaviour, and I absolutely loved it. Sonja, you have helped me obtain essential experience in observing chimpanzees, thank you, I have learned a lot from you.

Mijn lieve vrienden, bedankt voor alle mooie momenten, het vieren van het leven. Op deze plek is het onmogelijk om iedereen te bedanken, maar een aantal dierbaren wil ik noemen. Marike, voor de muziek en fijne gesprekken, Gerrie, voor de prikkelende filosofie en de natuur, het Weerwolf genootschap, voor de heerlijke vakanties en avontuurlijke fietstochten, Timme, voor je relativerende humor, Dorrie, voor je inspirerende levenslust en bizar mooie trailruns – van dit alles heb ik intens genoten tijdens mijn soms toch uitdagende onderzoekstraject.

Lieve pino's, jullie zijn als een warm nest voor mij. Met jullie staat de tijd stil, we zijn vrienden geworden vanaf het moment dat we elkaar ontmoetten en zullen dat altijd blijven. Thijs, heel bijzonder dat jij naast me staat als paranimf.

Mijn schoonouders, jullie interesse in mijn werk is weerspiegeld in een doos vol krantenknipsels. Hartelijk dank voor de leuke gesprekken, jullie betrokkenheid en warmte, ik voel me ontzettend thuis bij jullie. Maartje, Jasper, Hester, Erik, Arjen en Inge, ik had het niet fijner kunnen treffen met mijn extended family.

Mijn ouders, jullie onvoorwaardelijke liefde heeft mij altijd gesterkt, en ook al doe ik alles op afstand, ik ben jullie hier altijd dankbaar voor geweest en zal dat ook altijd blijven. Angela, Christian en Patrick, jullie zijn (als) mijn sibling apen, altijd betrokken en behulpzaam, heel veel dank daarvoor.

Lieve Jennie, mijn vriendin, mijn vrouw. Zonder jou had ik mijn droombaan nooit kunnen realiseren. Vanaf het moment dat we elkaar leerden kennen sta je voor me klaar, help je me mezelf te ontplooien, ken je me beter dan ikzelf. Mijn vele, langdurige verblijven in Zambia zijn zwaar geweest, en hoewel je dat al voorzag, ben je me toch altijd blijven steunen. Elke dag is mooier met jou samen, waar we ook zijn, jouw liefde maakt mij de gelukkigste man die ik maar zijn kan.

Mijn nieuwe favoriete primaatje, lieve Elias, wat een geluk dat we jou hebben mogen verwelkomen! Ik ben apetrots, de koning te rijk, met jou in ons midden.

Curriculum Vitae

Eduard Johannes Cornelis van Leeuwen has studied Mental Health Sciences and Psychology at the University of Maastricht, the Netherlands. After graduating from Maastricht University, he started crossing the bridge between human psychology and the study of non-human animal behaviour by volunteering for the position of research assistant at a chimpanzee sanctuary in Zambia called Chimfunshi Wildlife Orphanage Trust. This step led him to collaborations with primate research groups in Portsmouth and Cambridge, and via temporary research positions at Leiden University and the VU University of Amsterdam, he was invited to join the Max Planck junior research group called Comparative Cognitive Anthropology. For his doctoral thesis, he conducted research at Chimfunshi (Zambia) and the Wolfgang Köhler Primate Research Center (Germany). Edwin has recently finished his first post-doctoral position at the Department of Developmental Psychology of the University of Jena (Germany) and currently works as a post-doctoral research fellow at the School for Psychology and Neuroscience in St. Andrews (Scotland), continuing his research on chimpanzee dynamics at the Chimfunshi Wildlife Orphanage Trust (Zambia).

List of Publications

van Leeuwen, E. J. C., Kendal, R. L., Tennie, C. & Haun, D. B. M. (Accepted). Conformity and its look-a-likes, *Animal Behaviour*.

Coultas, J. C., & van Leeuwen, E. J. C. (2015). Conformity: Definitions, Types and Evolutionary grounding. In Zeigler-Hill, V., Welling, L., & Shackelford, T. K. (Eds.), *Evolutionary Perspectives on Social Psychology*. Springer, New York.

van Leeuwen, E. J. C., Call, J. & Haun, D. B. M. (2014). Human children rely more on social information than chimpanzees, *Biology Letters*.

van Leeuwen, E. J. C., & Haun, D. B. M. (2014). Conformity without majority? The case for demarcating social from majority influences, *Animal Behaviour*.

van Leeuwen, E. J. C., Cronin, K. A. & Haun, D. B. M. (2014). A group-specific arbitrary tradition in chimpanzees (*Pan troglodytes*), *Animal Cognition*.

Cronin, K. A., van Leeuwen, E. J. C., Vreeman, V., & Haun, D. B. M. (2014). Population-level variability in the social climates of four chimpanzee societies, *Evolution & Human Behavior*. Doi:10.1016/j.evolhumbehav.2014.05.004

Cronin, K. A., Pieper, B. A., van Leeuwen, E. J. C., Mundry, R., & Haun, D. B. M. (2014). Problem solving in the presence of others: How rank and relationship quality impact resource acquisition in chimpanzees (*Pan troglodytes*), *PLoS ONE*. Doi:10.1371/journal.pone.0093204

van Leeuwen, E. J. C., Cronin, K. A., Schütte, S., Call, J. & Haun, D. B. M. (2013). Chimpanzees flexibly adjust their behavior in order to maximize payoffs, not to conform to majorities, *PLoS ONE*. Doi:10.1371/journal.pone.0080945

van Leeuwen, E. J. C., Mulenga, I. C. & Lisensky, D. C. (2013). Early social deprivation negatively affects social skill acquisition in chimpanzees (*Pan troglodytes*), *Animal Cognition*. Doi:10.1007/s10071-013-0672-5

van Leeuwen, E. J. C. & Haun, D. B. M. (2013). Conformity in nonhuman primates: Fad or Fact? *Evolution & Human Behavior*. Doi:10.1016/j.evolhumbehav.2012.07.005

Haun, D. B. M., van Leeuwen, E. J. C. & Edelson, M. (2013). Majority influence in children and other animals, *Developmental Cognitive Neuroscience*. Doi:10.1016/j.dcn.2012.09.003

van Leeuwen, E. J. C., Cronin, K. A., Haun, D. B. M., Mundry, R. & Bodamer, M. D. (2012). Neighbouring chimpanzee communities show different preferences in

social grooming behaviour, *Proceedings of the Royal Society B: Biological Sciences*.
Doi:10.1098/rspb.2012.1543

van Leeuwen, E. J. C., Zimmerman, E., & Davila Ross, M. (2011). Responding to inequities: gorillas try to maintain their competitive advantage during play fights, *Biology Letters*. Doi:10.1098/rsbl.2010.0482

Cronin, K. A., van Leeuwen, E. J. C., Mulenga, I. C., & Bodamer, M. D. (2011). Behavioral response of a chimpanzee mother toward her dead infant, *American Journal of Primatology*, 73(5), 415-421. Doi:10.1002/ajp.20927.

Dunbar, R, Baron, R., Frangou, A., Pearce, van Leeuwen, E. J. C., Stow, J., Partridge, G., Macdonald, I., Barra, V., & van Vugt, M (2011). Social laughter is correlated with an elevated pain threshold, *Proceedings of the Royal Society B: Biological Sciences*. Doi:10.1098/rspb.2011.1373

Rieffe, C., Oosterveld, P., Meerum Terwogt, M., Mootz, S., van Leeuwen, E. J. C. & Stockmann, A.P.A.M. (2010). Emotion regulation and internalizing symptoms in children with Autism Spectrum Disorders, *Autism*.
Doi:10.1177/1362361310366571

MPI Series in Psycholinguistics

1. The electrophysiology of speaking: Investigations on the time course of semantic, syntactic, and phonological processing. *Miranda van Turenhout*
2. The role of the syllable in speech production: Evidence from lexical statistics, metalinguistics, masked priming, and electromagnetic midsagittal articulography. *Niels O. Schiller*
3. Lexical access in the production of ellipsis and pronouns. *Bernadette M. Schmitt*
4. The open-/closed-class distinction in spoken-word recognition. *Alette Haveman*
5. The acquisition of phonetic categories in young infants: A self-organising artificial neural network approach. *Kay Behnke*
6. Gesture and speech production. *Jan-Peter de Ruiter*
7. Comparative intonational phonology: English and German. *Esther Grabe*
8. Finiteness in adult and child German. *Ingeborg Lasser*
9. Language input for word discovery. *Joost van de Weijer*
10. Inherent complement verbs revisited: Towards an understanding of argument structure in Ewe. *James Essegbey*
11. Producing past and plural inflections. *Dirk Janssen*
12. Valence and transitivity in Saliba: An Oceanic language of Papua New Guinea. *Anna Margetts*
13. From speech to words. *Arie van der Lugt*
14. Simple and complex verbs in Jaminjung: A study of event categorisation in an Australian language. *Eva Schultze-Berndt*
15. Interpreting indefinites: An experimental study of children's language comprehension. *Irene Krämer*
16. Language-specific listening: The case of phonetic sequences. *Andrea Weber*
17. Moving eyes and naming objects. *Femke van der Meulen*
18. Analogy in morphology: The selection of linking elements in Dutch compounds. *Andrea Krott*
19. Morphology in speech comprehension. *Kerstin Mauth*
20. Morphological families in the mental lexicon. *Nivja H. de Jong*
21. Fixed expressions and the production of idioms. *Simone A. Sprenger*
22. The grammatical coding of postural semantics in Goemai (a West Chadic language of Nigeria). *Birgit Hellwig*
23. Paradigmatic structures in morphological processing: Computational and cross-linguistic experimental studies. *Fermín Moscoso del Prado Martín*
24. Contextual influences on spoken-word processing: An electrophysiological approach. *Daniëlle van den Brink*
25. Perceptual relevance of prevoicing in Dutch. *Petra M. van Alphen*
26. Syllables in speech production: Effects of syllable preparation and syllable frequency. *Joana Cholin*
27. Producing complex spoken numerals for time and space. *Marjolein Meeuwissen*

28. Morphology in auditory lexical processing: Sensitivity to fine phonetic detail and insensitivity to suffix reduction. *Rachèl J. J. K. Kemps*
29. At the same time...: The expression of simultaneity in learner varieties. *Barbara Schmiedtová*
30. A grammar of Jalonke argument structure. *Friederike Lüpke*
31. Agrammatic comprehension: An electrophysiological approach. *Marlies Wassenaar*
32. The structure and use of shape-based noun classes in Miraña (North West Amazon). *Frank Seifart*
33. Prosodically-conditioned detail in the recognition of spoken words. *Anne Pier Salverda*
34. Phonetic and lexical processing in a second language. *Mirjam Broersma*
35. Retrieving semantic and syntactic word properties. *Oliver Müller*
36. Lexically-guided perceptual learning in speech processing. *Frank Eisner*
37. Sensitivity to detailed acoustic information in word recognition. *Keren B. Shatzman*
38. The relationship between spoken word production and comprehension. *Rebecca Özdemir*
39. Disfluency: Interrupting speech and gesture. *Mandana Seyfeddinipur*
40. The acquisition of phonological structure: Distinguishing contrastive from non-contrastive variation. *Christiane Dietrich*
41. Cognitive cladistics and the relativity of spatial cognition. *Daniel B.M. Haun*
42. The acquisition of auditory categories. *Martijn Goudbeek*
43. Affix reduction in spoken Dutch. *Mark Pluymaekers*
44. Continuous-speech segmentation at the beginning of language acquisition: Electrophysiological evidence. *Valesca Kooijman*
45. Space and iconicity in German Sign Language (DGS). *Pamela Perniss*
46. On the production of morphologically complex words with special attention to effects of frequency. *Heidrun Bien*
47. Crosslinguistic influence in first and second languages: Convergence in speech and gesture. *Amanda Brown*
48. The acquisition of verb compounding in Mandarin Chinese. *Jidong Chen*
49. Phoneme inventories and patterns of speech sound perception. *Anita Wagner*
50. Lexical processing of morphologically complex words: An information-theoretical perspective. *Victor Kuperman*
51. A grammar of Savosavo, a Papuan language of the Solomon Islands. *Claudia Wegener*
52. Prosodic structure in speech production and perception. *Claudia Kuzla*
53. The acquisition of finiteness by Turkish learners of German and Turkish learners of French: Investigating knowledge of forms and functions in production and comprehension. *Sarah Schimke*
54. Studies on intonation and information structure in child and adult German. *Laura de Ruiter*
55. Processing the fine temporal structure of spoken words. *Eva Reinisch*
56. Semantics and (ir)regular inflection in morphological processing. *Wieke Tabak*
57. Processing strongly reduced forms in casual speech. *Susanne Brouwer*

58. Ambiguous pronoun resolution in L1 and L2 German and Dutch. *Miriam Ellert*
59. Lexical interactions in non-native speech comprehension: Evidence from electroencephalography, eye-tracking, and functional magnetic resonance imaging. *Ian FitzPatrick*
60. Processing casual speech in native and non-native language. *Annelie Tuinman*
61. Split intransitivity in Rotokas, a Papuan language of Bougainville. *Stuart Robinson*
62. Evidentiality and intersubjectivity in Yurakaré: An interactional account. *Sonja Gipper*
63. The influence of information structure on language comprehension: A neurocognitive perspective. *Lin Wang*
64. The meaning and use of ideophones in Siwu. *Mark Dingemanse*
65. The role of acoustic detail and context in the comprehension of reduced pronunciation variants. *Marco van de Ven*
66. Speech reduction in spontaneous French and Spanish. *Francisco Torreira*
67. The relevance of early word recognition: Insights from the infant brain. *Caroline Junge*
68. Adjusting to different speakers: Extrinsic normalization in vowel perception. *Matthias J. Sjerps*
69. Structuring language. Contributions to the neurocognition of syntax. *Katrien R. Segaert*
70. Infants' appreciation of others' mental states in prelinguistic communication: A second person approach to mindreading. *Birgit Knudsen*
71. Gaze behavior in face-to-face interaction. *Federico Rossano*
72. Sign-spatiality in Kata Kolok: how a village sign language of Bali inscribes its signing space. *Conny de Vos*
73. Who is talking? Behavioural and neural evidence for norm-based coding in voice identity learning. *Attila Andics*
74. Lexical processing of foreign-accented speech: Rapid and flexible adaptation. *Marijt Witteman*
75. The use of deictic versus representational gestures in infancy. *Daniel Puccini*
76. Territories of knowledge in Japanese conversation. *Kaoru Hayano*
77. Family and neighbourhood relations in the mental lexicon: A cross-language perspective. *Kimberley Mulder*
78. Contributions of executive control to individual differences in word production. *Zeshu Shao*
79. Hearing speech and seeing speech: Perceptual adjustments in auditory-visual processing. *Patrick van der Zande*
80. High pitches and thick voices: The role of language in space-pitch associations. *Sarah Dolscheid*
81. Seeing what's next: Processing and anticipating language referring to objects. *Joost Rommers*
82. Mental representation and processing of reduced words in casual speech. *Iris Hanique*
83. The many ways listeners adapt to reductions in casual speech. *Katja Poellmann*

84. Contrasting opposite polarity in Germanic and Romance languages: Verum Focus and affirmative particles in native speakers and advanced L2 learners. *Giuseppina Turco*
85. Morphological processing in younger and older people: Evidence for flexible dual-route access. *Jana Reifegerste*
86. Semantic and syntactic constraints on the production of subject-verb agreement. *Alma Veenstra*
87. The acquisition of morphophonological alternations across languages. *Helen Buckler*
88. The evolutionary dynamics of motion event encoding. *Annemarie Verkerk*
89. Rediscovering a forgotten language. *Jiyoun Choi*
90. The road to native listening: Language-general perception, language-specific input. *Sho Tsuji*
91. Infants' understanding of communication as participants and observers. *Gudmundur Bjarki Thorgrímsson*
92. Information structure in Avatime. *Saskia van Putten*
93. Switch reference in Whitesands. *Jeremy Hammond*
94. Machine learning for gesture recognition from videos. *Binyam Gebrekidan Gebre*
95. Acquisition of spatial language by signing and speaking children: a comparison of Turkish sign language (TID) and Turkish. *Beyza Sumer*
96. An ear for pitch: on the effects of experience and aptitude in processing pitch in language and music. *Salomi Savvatia Asaridou*
97. Incrementality and Flexibility in Sentence Production. *Maartje van de Velde*
98. Social learning dynamics in chimpanzees: Reflections on animal culture. *Edwin van Leeuwen*